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ALVARIÑO, A.

1990. Chaetognatha. *In* K. G. and R. G. Adiyodi (eds.), Reproductive Biology of Invertebrates, Vol. IV, Part B, Fertilization, Development, and Parental Care, pp. 255-282. Oxford & IBH Publishing Co. Pvt. Ltd. 9001

———.

1990. Chaetognatha. *In* K. G. and R. G. Adiyodi (eds.), Reproductive Biology of Invertebrates, Vol. V, Sexual Differentiation and Behavior, pp. 425-270. Oxford & IBH Publishing Co. Pvt. Ltd.. 9002

BAKUN, A.

1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198-201. 9003

BAKUN, A., AND R. H. PARRISH.

1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). J. Cons. int. Explor. Mer. 46:269-283. 9004

BARLOW, J.

1990. A birth-interval model for estimating cetacean reproductive rates from resighting data. Rep. int. Whal. Commn (special issue 12):155-160. 9005

BUSHNELL, P. G., R. W. BRILL, AND R. E. BOURKE.

1990. Cardiorespiratory responses of skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares*; and bigeye tuna, *Thunnus obesus*, to acute reductions of ambient oxygen. Can. J. Zool. 68:1857-1865. 9006

BUTLER, J. L.

1990. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California Current during 1980-84. Fish. Bull., U.S. 87:645-652.. 9007

CLARKE, R. P., AND S. S. YOSHIMOTO.

1990. Application of the Leslie model to commercial catch and effort of the slipper lobster, *Scyllarides squammosus*, fishery in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 52(2):1-7. 9008

COHEN, D. M., R. H. ROSENBLATT, AND H. G. MOSER.

1990. Biology and description of a bythitid fish from deep-sea thermal vents in the tropical eastern Pacific. Deep-Sea Res. 37(2):267-283.. 9009

DIZON, A. E., AND J. E. ROSENBERG.

1990. We don't care, Professor Einstein, the instructions to the authors specifically said double-spaced. *In* J. R. Hunter (ed.), Writing for Fishery Journals, pp. 65-74. Am. Fish. Soc. 9010

TABLE OF CONTENTS (CONTINUED)

ELIASON, J. J., T. C. JOHANOS, AND M. A. WEBBER.
1990. Parturition in the Hawaiian monk seal (*Monachus schauinslandi*). Mar. Mammal Sci. 6(2):146-151. 9011

EVERSON, A. R., H. A. WILLIAMS, AND B. M. ITO.
1990. Maturation and reproduction in two Hawaiian eteline snappers, uku, *Aprion virescens,* and onaga, *Etelis coruscans.* Fish. Bull., U.S. 87(4):877-888. 9012

FIEDLER, P. C., AND R. M. LAURS.
1990. Variability of the Columbia River plume observed in visible and infrared satellite imagery. Int. J. Remote Sensing 11(6):999-1010. 9013

GERRODETTE, T., AND D. P. DEMASTER.
1990. Quantitative determination of optimum sustainable population level. Mar. Mammal Sci. 6(1):1-16. 9014

GERRODETTE, T., AND W. G. GILMARTIN.
1990. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. Conservation Biol. 4(4):423-430. 9015

HARMON, R. F., AND M. P. SEKI.
1990. *Iridoteuthis iris* (Cephalopoda: Sepiolidae): New records from the central North Pacific and first description of the adults. Pac. Sci. 44:171-179. 9016

HERRICK, S. F., JR., AND D. SQUIRES.
1990. On measuring fishing fleet productivity: development and demonstration of an analytical framework. Fish. Bull., U.S. 88(1):85-94. 9017

HIGHTOWER, J. E.
1990. Multispecies harvesting policies for Washington-Oregon-California rockfish trawl fisheries. Fish. Bull., U.S. 88(4):645-656. 9018

HOBBS, R. C., L. W. BOTSFORD, AND R. G. KOPE.
1990. Bioeconomic evaluation of the culture/stocking concept for California halibut. *In* C. W. Haugen (ed.), The California halibut, *Paralichthys californicus*, resource and fisheries, pp. 417-449. Calif. Dep. Fish Game Fish. Bull. 174. 9019

HOLLAND, K. N., R. BRILL, AND R. K. C. CHANG.
1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fish. Bull., U.S. 88(2):397-402. 9020

TABLE OF CONTENTS (CONTINUED)

———————.

1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull., U.S. 88(3):493-507. 9021

HOLT, R. S., AND S. N. SEXTON.

1990. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. Fish. Bull., U.S. 88(1):105-111. 9022

———————

1990. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1987 data. Rep. int. Whal. Commn 39:347-351. 9023

HOLTS, D., AND D. BEDFORD.

1990. Activity patterns of striped marlin in the Southern California Bight. *In* R. H. Stroud (ed.), Planning the future of billfishes, pp. 81-93. Proc. Int. Billfish Symp., Kailua-Kona, HI, August 1-5, 1988. Mar. Rec. Fish. 13, Cont. Pap., Part 2. 9024

HUNTER, J.

1990. Statistical aspects of fishery papers. *In* J. Hunter (ed.), Writing for fishery journals, pp. 1-79. Am. Fish. Soc., Bethesda, MD. 9025

HUNTER, J. R., J. L. BUTLER, C. KIMBRELL, AND E. A. LYNN.

1990. Bathymetric patterns in size, age, sexual maturity, water content, and caloric density of Dover sole, *Microstomus pacificus*. Calif. Coop. Oceanic Fish. Invest. Rep. 31:132-144. 9026

KOPE, R. G., AND L. W. BOTSFORD.

1990. Determination of factors affecting recruitment of chinook salmon, *Oncorhynchus tshawytscha*, in central California. Fish. Bull., U.S. 88(2):257-269. 9027

LOWRY, M. S., AND R. L. FOLK.

1990. Sex determination of the California sea lion, (*Zalophus californianus californianus*), from canine teeth. Mar. Mammal Sci. 6(1):25-31. 9028

LOWRY, M. S., C. W. OLIVER, C. MACKY, AND J. B. WEXLER.

1990. Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981-86. Fish. Bull., U.S. 88(3):509-521. 9029

LYNN, R. J., AND J. J. SIMPSON.

1990. The flow of the undercurrent over the continental borderland off southern California. J. Geophys. Res. 95(C8):12,995-13,008. 9030

TABLE OF CONTENTS (CONTINUED)

MACFARLANE, R. B., H. R. HARVEY, M. J. BOWERS, AND J. S. PATTON.
1990. Serum lipoproteins in striped bass, (*Morone saxatillis*): effects of starvation. Can. J. Fish. Aquat. Sci. 47(4):739-745. 9031

MANGEL, M., AND P. E. SMITH.
1990. Presence-absence sampling for fisheries management. Can. J. Fish. Aquat. Sci. 47:1875-1887. 9032

MATSUI, T., S. KATO, AND S. E. SMITH.
1990. Biology and potential use of Pacific grenadier, *Coryphaenoides acrolepis*, off California. Mar. Fish. Rev. 52(3):1-17. 9033

MENDELSSOHN, R.
1990. Relating fisheries to the environment in the Gulf of Guinea: information, causality and long-term memory. *In* P. Cury and C. Roy (eds.), The Impact of Climatic Variations on Pelagic Fish stocks of West Africa, pp. 446-465. ORSTOM, Dakar. 9034

MORALES-NIN, B., AND S. RALSTON.
1990. Age and growth of *Lutjanis kasmira* (Forskål) in Hawaiian waters. J. Fish. Biol. 36:191-203. 9035

MUENCH, R. D., J. T. GUNN, AND D. M. HUSBY.
1990. The Weddell-Scotia confluence in midwinter. J. Geophys. Res. 95(C10):18,177-18,190. 9036

MUNDY, B. C.
1990. Development of larvae and juveniles of the alfonsins, *Beryx splendens* and *B. decadactylus* (Berycidae, Beryciformes). Bull. of Mar. Sci. 46(2):257-273. 9037

MYRICK, A. C., JR., AND L. H. CORNELL.
1990. Chapter 34: Calibrating dental layers in captive bottlenose dolphins from serial tetracycline labels and tooth extractions. *In* S. Leatherwood and R. R. Reeves (eds.), The Bottlenose Dolphin, pp, 587-608. Academic Press, Inc., NY. 9038

ORR, B. K., W. W. MURDOCH, AND J. R. BENCE.
1990. Population regulation, convergence, and cannibalism in *Notonecta* (Hemiptera). Ecology 71(1):68-82. 9039

PARKS, W. W., P. J. DONLEY, AND S. F. HERRICK, JR.
1990. U.S. trade in tuna for canning, 1987. Mar. Fish. Rev. 52(1):14-22. 9040

PERRIN. W. F.
1990. Annex H. Report of the Sub-Committee on Small Cetaceans. Rep. int. Whal. Commn 40:144-153. 9041

TABLE OF CONTENTS (CONTINUED)

____

1990. Annex Q. Report of the Steering Committee on the proposed meeting on Mortality of Cetaceans in Fishing Nets and Traps. Rep. int. Whal. Commn 40:177. 9042

____

1990. Report of the Cetacean Specialist Group. Species (Newsl. Species Surviv. Commn.) 13-14:71-72.. 9043

____

1990. *Steno attenuatus* gray, 1846 (currently *Stenella attenuata*; Mammalia, Cetacea): proposed conservation of the specific name. Bull. Zool. Nomencl. 47(1):32-37.. 9044

____

1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc. Biol. Soc. Wash. 103(2):453-463. 9045

PITMAN, R. L., AND L. T. BALLANCE.
1990. Daytime feeding by Leach's Storm-Petrel on a midwater fish in the eastern tropical Pacific. The Condor 92:524-527. 9046

POLOVINA, J. J.
1990. Application of yield-per-recruit and surplus production models to fishery enhancement through juvenile releases. *In* A. K. Sparks (ed.), Marine farming and enhancement, pp. 29-33. NOAA Tech. Rep. NMFS 85.. 9047

POLOVINA, J. J., R. A. BENCO, A. H. CARLOT, E. CILLAURREN, P. DALZELL, N. HOWARD, D. KOBAYASHI, T. F. LATU, P. LOKANI, G. NATH, H. PITIALE, A. SESEWA, R. SHOMURA., T. SUA, G. TIROBA, AND S. TULUA.
1990. Introduction and summary of methods and results from the Tropical Stock Assessment Workshop. *In* J. J. Polovina and R. S. Shomura (eds.), United States Agency for International Development and National Marine Fisheries Service Workshop on Tropical Fish Stock Assessment, July 5-26, 1989, Honolulu, HI, pp. 1-6. 9048

POOLEY, S.
1990. Limited entry and Hawaii's fisheries interaction problem. *In* C. M. Dewees and E. Ueber (eds.), Effects of different fishery management schemes on bycatch, joint catch, and discards, pp 40-41. Report No. T-CSGCP-019 (Abstract), California Sea Grant College, University of California, La Jolla, CA. 9049

TABLE OF CONTENTS (CONTINUED)

RALSTON, S.
1990. Size selection of snappers (Lutjanidae) by hook and line gear. Can. J. Fish. Aquat. Sci. 47:696-700. 9050

RATTY, F. J., R. M. LAURS, AND R. M. KELLY.
1990. Gonad morphology, histology, and spermatogenesis in South Pacific albacore tuna *Thunnus alalunga* (Scombridae). Fish Bull., U.S. 88(1):207-216. 9051

REILLY, S. B.
1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1-11. 9052

REILLY, S. B., AND V. G. THAYER.
1990. Blue whale, (*Balaenoptera musculus*), distribution in the eastern tropical Pacific. Mar. Mammal Sci. 6(4):265-277. 9053

SEEB, L. W., J. E. SEEB, AND J. J. POLOVINA.
1990. Genetic variation in highly exploited spiny lobster, *Panulirus marginatus*, populations from the Hawaiian Archipelago. Fish. Bull., U.S. 88(4): 712-718. 9054

SEGERSON, K., AND D. SQUIRES.
1990. On the measurement of economic capacity utilization for multi-product industries. J. Econometrics 44:347-361.. 9055

SMITH, P. E.
1990. Monitoring interannual changes in spawning area of Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 31:145-151. 9056

SMITH, S. E., AND N. J. ABRAMSON.
1990. Leopard shark, *Triakis semifasciata*, distribution, mortality rate, yield and stock replenishment estimates based on a tagging study in San Francisco Bay. Fish. Bull., U.S. 88:371-381.. 9057

SOMERTON, D. A.
1990. Baitfish stock assessment using the egg production method: an application on the Hawaiian anchovy or nehu *Encrasicholina purpurea*. *In* S. J. M. Blaber and J. W. Copland (eds.), Tuna Baitfish in the Indo-Pacific region: Proceedings of a Workshop, Honiara, Solomon Islands, 11-13 December 1989, pp. 152-158. Inkata Press PTY LTD Publ., Victoria, Australia.. 9058

TABLE OF CONTENTS (CONTINUED)

SQUIRE, J. L., JR.
1990. Distribution and apparent abundance of the basking shark, *Cetorhinus maximus*, off the central and southern California coast, 1962-85. Mar. Fish. Rev. 52(2):8-11. 9059

SQUIRE, J. L., AND D. W. K. AU.
1990. Striped marlin in the northeast Pacific—A case for local depletion and core area management. *In* R. H. Stroud (ed.), Planning the future of billfishes. Proc. Int. Billfish Symp., Kailua-Kona, HI, August 1-3, 1989, pp. 199-214. Mar. Rec. Fish. 13, Cont. Pap., Part 2. 9060

SQUIRE, J. L., AND Z. SUZUKI.
1990. Migration trends of striped marlin (*Tetrapturus audax*) in the Pacific Ocean. *In* R. H. Stroud (ed.), Planning the future of billfishes. Proc. Int. Billfish Symp., Kailua-Kona, HI, August 1-3, 1989, pp. 67-80. Mar. Rec. Fish. 13, Cont. Pap., Part 2. 9061

SUND, P. N., AND J. G. NORTON.
1990. Interpreting long-term fish landings records: environment and/or exploitation? *In* J. I. Betancourt, and A. M. MacKay (eds.), Proceedings of the Sixth Annual Pacific Climate (PACLIM) Workshop, March 5-8, 1989, pp. 71-75. California Department of Water Resources, Interagency Ecological Studies Program Technical Report 23. 9062

THOMAS, J. A., P. W. B. MOORE, P. E. NACHTIGALL, AND W. G. GILMARTIN.
1990. A new sound from a stranded pygmy sperm whale. Aquat. Mammal. 16(1):28-30. 9063

THOMSON, C. J.
1990. The market for fish meal and oil in the United States: 1960-1988 and future prospects. Calif. Coop. Oceanic Fish. Invest. Rep. 31:124-131. 9064

UCHIYAMA, J. H., AND J. D. SAMPAGA.
1990. Age estimation and composition of pelagic armorhead *Pseudopentaceros wheeleri* from the Hancock Seamounts. Fish. Bull., U.S. 88(1):217-222. 9065

UEBER, E.
1990. Using mesh sizes to reduce discards. *In* C. M. Dewees and E. Ueber (eds.), Effects of different fishery management schemes on bycatch, joint catch, and discards, pp 30-31. Report No. T-CSGCP-019, California Sea Grant College, University of California, La Jolla, CA.. 9066

TABLE OF CONTENTS (CONTINUED)

UEBER, E., AND A. MACCALL.
1990. The collapse of California's sardine fishery. *In* M. H. Glantz and L. E. Feingold (eds.), Climate variability, climate change and fisheries, pp. 17-23. National Center for Atmospheric Research, Boulder, CO.. 9067

WESTLAKE, R. L., AND W. G. GILMARTIN.
1990. Hawaiian monk seal pupping locations in the Northwestern Hawaiian Islands. Pac. Sci. 44(4):366-383. 9068

WILSON, C. D., AND G. W. BOEHLERT.
1990. Acoustic measurement of micronekton distribution over Southeast Hancock Seamount, central Pacific Ocean. *In* S. P. Singal (ed.), Acoustic Remote Sensing of the Atmosphere and Oceans, pp. 222-229. Tata-McGraw Hill Publ., New Delhi. 9069

____

1990. The effects of different otolith ageing techniques on estimates of growth and mortality for the splitnose rockfish, *Sebastes diploproa*, and canary rockfish, *S. pinniger*. Calif. Fish Game 76:146-160. 9070

YOKLAVICH, M. M., AND K. M. BAILEY.
1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. Mar. Ecol. Prog. Ser. 64:13-23. 9071

The following publications are not included in the Collected Reprints 1990.

ALVARIÑO, A., J. M. WOJTAN, AND M. R. MARTINEZ.
1990. Antarctic siphonophores from plankton samples of the United States Antarctic research program: *Eltanin* cruises for spring, summer, fall, and winter (Cruises 3-5, 8-23, 25-28, 30, 35, and 38). *In* L. S. Kornicker (ed.), Biology of the Antarctic Seas XX, pp. 1-436. Am. Geophys. Union, Antarctic Res. Ser. 49.

BAKUN, A.
1990. L'ocean et la variabilité des populations marines. *In* J. P. Troadec (ed.), L'Homme et les Écosystems Halieutiques, pp. 155-187. Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER), Paris.

TABLE OF CONTENTS (CONTINUED)

BALAZ, G. H., E. D. GOMEZ, AND N. B. LINSLEY.
1990. Marine turtle postage stamps of the world—promoting conservation. *In* T. H. Richardson, J. I. Richardson, and M. Donnelly (compilers), Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation, pp. 215-219. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SEFC-278.

BENCE, J. R., AND J. E. HIGHTOWER.
1990. Appendix J: Status of bocaccio in the Conception/Monterey/Eureka INPFC areas in 1990. *In* Status of the Pacific Coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Pacific Fishery Management Council, Portland, OR.

DEWEES, C. M., AND E. UEBER (EDS.)
1990. Effects of different fishery management schemes on bycatch, joint catch, and discards. Report No. T-CSGCP-019, California Sea Grant College, University of California, La Jolla, CA, 55 p.

ECHEVERRIA, T. W., W. H. LENARZ, AND C. A. REILLY.
1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-147, 125 p.

FIEDLER, P. C., L. J. LIERHEIMER, S. B. REILLY, S. N. SEXTON, R. S. HOLT, AND D. P. DEMASTER.
1990. Atlas of eastern tropical Pacific oceanographic variability and cetacean sightings, 1986-1989. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-144, 142 p.

HENDERSON, J. R., AND M. R. FINNEGAN.
1990. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi*, and captive maintenance project at Kure Atoll, 1988. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-150, 10 p.

HIGHTOWER, J. E.
1990. Biomass-based models and harvesting policies for Washington-Oregon-California rockfish stocks with correlated recruitment patterns. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-137, 39 p.

HIGHTOWER, J. E., AND W. H. LENARZ.
1990. Appendix F: Status of the widow rockfish fishery in 1990. *In* Status of the Pacific Coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland, OR.

TABLE OF CONTENTS (CONTINUED)

HILL, P. SCOTT, A. JACKSON, AND T. GERRODETTE.

1990. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan* July 29-December 7, 1989. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-142, 143 p.

———

1990. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur* July 29-December 7, 1989. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-143, 132 p.

HINKLEY, S., K. M. BAILEY, S. J. PICQUELLE, M. M. YOKLAVICH, AND J. D. SCHUMACHER.

1990. Realistic estimation of mortality rates of larval walleye pollock in the Gulf of Alaska as determined from field sampling. (Abstract) Eos 71:93.

HOBSON, E. S., AND E. H. CHAVE.

1990. Hawaiian reef animals. Revised edition. University of Hawaii Press, Honolulu, HI, 137 p.

HOLLAND, R. C.

1990. A personal computer based system for analog-to-digital and serial communication data acquisition. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-152, 26 p.

HUNTER, J. (ED.).

1990. Writing for fishery journals. Am. Fish. Soc., Bethesda, MD, 102 p.

JACKSON, A. R.

1990. Summary of the 1988 U.S. tuna/porpoise observer data. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-149, 32 p.

JOHANOS, T. C., B. L. BECKER, M. A. BROWN, B. K. CHOY, L. M. HURUKI, R. E. BRAINARD, AND R. L. WESTLAKE.

1990. The Hawaiian monk seal on Laysan Island, 1988. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-151, 17 p.

LIERHEIMER, L. J., P. C. FIEDLER, S. B. REILLY, R. L. PITMAN, L. T. BALLANCE, S. C. BEAVERS, G. G. THOMAS, AND D. W. BEHRINGER.

1990. Report of ecosystem studies conducted during the 1989 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan* U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-139, 118 p.

TABLE OF CONTENTS (CONTINUED)

LIERHEIMER, L. J., P. C. FIEDLER, S. B. REILLY, R. L. PITMAN,
L. T. BALLANCE, S. C. BEAVERS, AND D. W. BEHRINGER.

1990. Report of ecosystem studies conducted during the 1989 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-140, 123 p.

MACCALL, A. D.

1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, Seattle, WA, 153 p.

METHOT, R., AND J. HIGHTOWER.

1990. Appendix B: Status of the West Coast sablefish stock in 1990 and recommendations to management in 1991. *In* Status of the Pacific Coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Pacific Fishery Management Council, Portland, OR.

OLIVER, C. W., AND E. F. EDWARDS.

1990. Effects of including in mortality estimates, dolphins categorized as either injured or of undetermined status. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-138, 51 p.

PEARSON, D. E., AND S. RALSTON.

1990. Trends in landings, species composition, length-frequency distribution and sex ratios of 11 species of rockfish (Genus *Sebastes*) from central and northern California. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-145, 65 p.

POLOVINA, J. J., AND R. S. SHOMURA (EDS.).

1990. United States Agency for International Development and National Marine Fisheries Service Workshop on Tropical Fish Stock Assessment, May 26, 1989, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-148, 143 p.

PRAGER, M. H., AND A. D. MACCALL.

1990. Biostatistical models of contaminant and climate influences on fish populations of the Southern California Bight. Report to Ocean Assessments Division, U.S. National Ocean Service. Old Dominion University Technical Report 90-04.

RALSTON, S., A. D. MACCALL, AND D. E. PEARSON.

1990. Appendix L: Reduction in mean length and exploitation of central and northern California rockfish. *In* Status of the Pacific Coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Stock assessment and fishery evaluation, 4 p., Appendix Volume 2. Pacific Fishery Management Council, Portland, OR.

TABLE OF CONTENTS (CONTINUED)

SCHWING, F. B., D. M. HUSBY, D. E. TRACY, S. V. RALSTON, AND W. H. LENARZ.
1990. Hydrographic conditions in the Gulf of the Farallones following the spring transition. EOS Trans. Am. Geophys. Union 71:1350.

SCHWING, F. B., S. RALSTON, D. M. HUSBY, AND W. H. LENARZ.
1990. The nearshore physical oceanography off the central California coast during May-June, 1989: A summary of CTD data from juvenile rockfish surveys. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-153, 10 p. + appendices.

SHOMURA, R. S., AND M. L. GODFREY (EDS.).
1990. Proceedings of the Second International Conference on Marine Debris, 2-7 April 1989, Honolulu, Hawaii. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-154, 862 p.

STEVENS, E. G., R. L. CHARTER, H. G. MOSER, AND C. A. MEYER.
1990. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1984. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-141, 157 p.

WINCHELL, J. M.
1990. Field manual for phocid necropsies (specifically *Monachus schauinslandi*). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-146, 54 p.

WYLLIE-ECHEVERRIA, T., W. H. LENARZ, AND C. A. REILLY.
1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-147, 125 p.

Book Reviews

MUNDY, B. C.
1990. The larvae of Indo-Pacific shorefishes, by Jeffrey M. Leis and Thomas Trnski. Copeia 1990:1196-1198.

PERRIN, W. F.
1990. River dolphins and the larger toothed whale. *In* S. H. Ridgway and R. Harrison (eds.), Handbook of Marine Mammals—Volume 4. Mar. Mamm. Sci. 6(4):356-358.

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12. CHAETOGNATHA

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I. INTRODUCTION

Analyses of the anatomy of the gonads and of changes in their functional features (see Alvariño, Volumes I and II) serve as useful tools to establish the behavioural and physiological aspects of reproduction in chaetognaths. The entire phylum is hermaphroditic. Hermaphroditism is an important character making special demands on the process of sperm transfer and the physiology of reproduction and development.

II. FERTILIZATION

The mature spermatozoa pass from the testes down the vas deferens to the seminal vesicles, and are transferred from the seminal vesicles to the seminal receptacle of another individual during copulation. It was once thought that the sperm were extruded to the water and that they reached the ovary by currents developed by ciliary movement at the opening of the oviducts. This possibility is excluded because there are no ciliary epithelia at the female genital openings in chaetognaths. It was then considered that the transport of the semen was accomplished by approximation of the opening of the seminal vesicles to the openings of the female ducts, and in that way the tail of one specimen would be under the trunk of the other and vice versa.

The chaetognaths do not normally shed spermatozoa freely into the water. There is copulation with transfer of sperm which are stored in the seminal receptacle, a tube attached to and along the length of the ovary (Fig. 1,c; see also Alvariño, Volume II). In the seminal receptacle, the sperm develop to a new stage of maturity. In many animals, series of steps or stages are observed in maturation of the sperm, i.e. from the stage it is formed to the stage it is ready to fecundate the ovum. The series of changes undergone by the sperm is not morphological, but involves their chemistry and cytology. It is considered that the ova, due to the proximity of the sperm, may obtain some organic substances and ions that are related to the activity

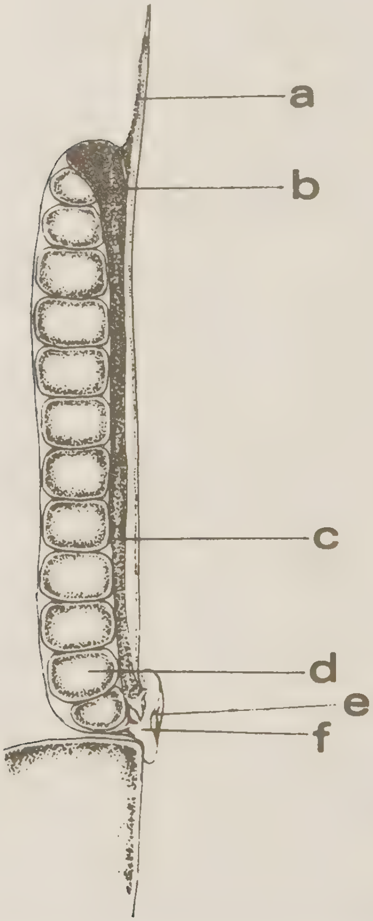

Fig. 1. Diagram of the ovary of a chaetognath (dorso-ventral view). a, Mesenteric conjunctival cord attaching the ovary to the body wall; b, ampulla of the seminal receptacle; c, seminal receptacle; d, ovum; e, vaginal opening (female sexual pore); f, uterus.

and oxygen-uptake of the sperm. This raises some problems concerning metabolism of the chaetognath spermatozoa. Clearly, further critical investigations are required on all aspects of sperm metabolism in chaetognaths, which might allow comparisons with spermatozoa of various invertebrates and vertebrates and on phylogenetic relationships of chaetognaths with other invertebrates.

In aquatic organisms, the output of gametes often achieves prodigious proportions; the animals become gamete-production factories during the breeding season. In chaetognaths, the trunk is almost completely filled with ova, and the tail segment with sperm. Diverse strategies and devices are used by animals to facilitate the encounter of partners and gamete union. They can be grouped into three broad categories: (1) elaboration of chemical agents to attract or trap the male gemetes;

(2) mechanical juxtaposition of gametes; (3) synchronization in production and release of gametes. The most useful and common patterns involve processes belonging to at least one of these categories, and in many cases a high level of efficiency is attained. However, the coupling of gametes involves also some elements of chance. Chaetognatha are hermaphrodite animals, and fertilization is by copulation (see Section III). Cytological, physiological, and histochemical details of the fertilization process are scarcely known. The chaetognaths expend sizeable portions of their biomass in the formation of the gametes, such that most of them die after reproduction.

III. MODES OF INSEMINATION

As outlined above (Section II), in chaetognaths, the spermatozoa are transferred by the vas deferens from the testis to the seminal vesicles where they are stored until copulation. During copulation, the sperm pass from the seminal vesicles into the seminal receptacles of the reciprocal partner. Muscular activity of the gonads may serve to accelerate the entry of sperm and the filling of the seminal receptacle; some chemotactic action may also take place.

Some hormones, secreted probably in the ovary in response to proximity of the sperm stored in the seminal receptacle, may induce oocyte growth and ovulation. Meanwhile, the sperm in the seminal receptacle reach the level of maturity needed to successfully fertilize the ova. The ova, released from the ovary, are carried into the uterus and vaginal cavity by a fluid current and by muscular contraction of the ovary. Fertilization *per se* seems to take place in the uterus or in the vaginal cavity, where opens the seminal receptacle (Fig. 1).

Statements by several authors (e.g. Ghirardelli, 1968) that the sperm pass through fine ducts from the seminal receptacle to the ova, stacked in rows along the ovary, are not accurate. There are no direct communications between the ovary and the seminal receptacle. Adult specimens have always their sperm duct filled with sperm, and no sperm is found inside the ovary proper. The ova do not develop into fertilized eggs while still in the ovary. In other words, no insemination occurs before the ova have been extruded to the uterus and vagina.

Cross-fertilization is the rule in Chaetognatha (Alvariño, 1965a, 1967a; Reeve and Cosper, 1975) though some instances of self-fertilization have also been reported (see Section IIIA below). The male gonads reach maturity earlier than the female gonads, a factor regulating the timing of copulation in these animals. In chaetognaths, the seminal fluid is emitted as a result of stimulation during copulation; only rarely is this discharged directly into the waters. When the sperm come in contact with sea water, the seminal fluid usually coagulates after a short time, and the mass could then be dispersed only with difficulty. Water-borne insemination appears most improbable, since it requires that two processes (viz. unstimulated oviposition and unstimulated seminal discharge) should occur simultaneously. Water-borne sperm in ocean cannot enter efficiently the seminal receptacles in chaetognaths. Under normal conditions, in epipelagic layers, the animals are distributed sufficiently close to each other with greater chances for encounter and copulation. However, mesopelagic and bathypelagic populations are not so abundant, and under those circumstances some incidental self-fertilization may occur. In *Eukrohnia*, for instance, the dorsal bending and curling of the posterior part of the lateral fins may assist the sperm in their passage from the seminal vesicles to the opening of the ovaries. However, eggs produced without copulation appear to be less viable than normally fertilized eggs.

Specimens of the benthic genus *Spadella*, successfully maintained in the laboratory, have been observed to engage in a behavioural sequence in which copulation occurs. According to Ghirardelli (1968), after a succession of quick movements and pushing, the two animals orient themselves in opposing directions; the seminal vesicles now attach reciprocally to the opening of the oviducts, and the copulating partners fill each others seminal receptacles with sperm.

A. Self-insemination

Self-fertilization appears to be less successful and efficient than cross-fertilization, producing only a small number of normal embryos. Spermatozoa of Chaetognatha are flagellate, but they do not have great powers for swimming, and do not move with great activity in sea water. However, there is a possibility that, aided by water movement, water-borne spermatozoa can effect fertilization at some distance from their point of release, the sperm reaching the seminal receptacle of individuals of the wrong species. But no hybrids have been so far observed in Chaetognatha. In copulating species, interspecific hybridization may be prevented by incompatibility of the genital apparatus.

Ghiselin (1969), who reviewed hermaphroditism in animals, recognized three possibilities in the fertilization process, and only one, the ‘classic’ low-density model, would apply to chaetognaths. It is evident that the ability to reproduce without the assistance of another animal would greatly increase the reproduction potential of a population of low density and low mobility. But neither of those characteristics would apply to Chaetognatha, abundant animals in the plankton (only second to copepods), mainly at the epipelagic layers, and seldom motionless. Other planktonic carnivores (euphasiids, amphipods) appear less abundant in the ocean than chaetognaths, and those animals are unisexual.

Self-fertilization was mentioned by Reeve (1970a,b) in isolated individuals confined to small dishes. Mature sperm will flow out into and swim about in the surrounding water as the seminal vesicle bursts and some sperm may enter the opening of the oviducts. The fact that this may happen does not imply it is the rule in nature. This is rare in *Sagitta hispida* (Reeve and Cosper, 1975): only 2 per cent of the animals, grown in isolation in small dishes, produced eggs. Self-insemination could nevertheless be more easily artificially induced by breaking open the seminal vesicles. Animals, isolated after they have been inseminated, would only lay one batch of fertile eggs; subsequent batches were nonfertile. These observations suggest that in chaetognaths self-insemination could provide a short-term survival mechanism in populations temporarily at very low densities. Since the general morphological characters of all planktonic and benthic-hypoplanktonic chaetognaths are similar, it may be expected that they generally resort to cross-fertilization only.

B. Spermatophore

No spermatophores are produced by Chaetognatha. Bundles of spermatozoa may sometimes coagulate to form a ball shortly on contact with sea water, and these have been mistaken by some investigators for spermatophores. Description of the presence of a 'spermatophore' at the region of the corona ciliata, for example by Ghirardelli (1968), and of streams of spermatozoa simultaneously moving caudally is questionable, In nature, it may be recalled, there is a harmonious relationship between anatomy and the mating process, in other words structure and function. What purpose would be served by placing one 'spermatophore' outside the body and releasing sperm free into the water ? It is also not clear why only one 'spermatophore' is produced whereas the animal has two seminal vesicles and two openings of the oviducts to conduct the semen to the seminal receptacle. In chaetognaths, the sperm obviously are passed from the seminal vesicles to fill the seminal receptacle of the recipient, and no sperm have been found stored inside the ovary as such, the tubular organ containing the ova.

In *Sagitta nagae,* a species propagating by cross-fertilization, Nagasawa and Marumo (1978) observed one to four 'spermatophores' attached to the body at the level of the anterior or posterior fins in animals collected at night, but none in animals from daylight collections. In the many hundreds of thousands of chaetognaths I examined (alive and preserved), I have never come across any 'spermatophores', though the seminal receptacles in many instances were indeed filled with sperm. I have also seen agglomerations or bundles of spermatozoa casually attached to various places on the body of the animal, but they were not spermatophores in the true sense of the term.

C. Copulation and Mating Behaviour

Extensive observations have been made by Reeve and Walter (1972b) on copulation and mating behaviour of *Sagitta hispida.* These authors found that two animals became attached to each other by their hoods at the start of the behavioural sequence; their bodies flexed and twisted about each other as they swam upward in spiralling motions, alternating with intervals of passivity and sinking down. The whole performance lasted from a few seconds to about 10 minutes. In about 59 couplings observed (Reeve and Walter, 1972b), the result was consistently that sperm appeared in the seminal receptacle of the animals, and the seminal vesicle in turn was empty.

The presence of peculiar formations on seminal vesicles in chaetognaths is far too constant to be void of any functional significance. These formations may be considered in some way to be copulatory organs, fitting the female genital orifices, thus making mating impossible between individuals of different species. Differences in morphology of mature seminal vesicles, seen in closely related species, would thus have value as a highly discriminative systematic characteristic.

The inability of various authors to find *Eukrohnia fowleri* or *E. bathyantarctica* with mature seminal vesicles in plankton collections is related to the small number of specimens analysed and to the depth from which the collections have been made. Ripe and full seminal vesicles break off easily, more so in specimens dredged from deep waters such as *E. fowleri* and *E. bathyantarctica,* due to change in pressure when brought to the surface waters.

IV. EGG-LAYING

The ova pass to the lowest part of the ovary, viz. uterus and vagina, where the duct of the seminal receptacle opens and releases the spermatozoa. As the ova reach the vagina they are fecundated by the spermatozoa, a process that apparently takes 20 to 30 minutes. Eggs of species of chaetognaths belonging to the genus of the highest evolutionary rank are probably the best equipped for survival (Alvariño, 1968).

Spadella eggs are laid in clusters of four to 12 or 16, attached to an elastic peduncle over a substratum (Vasiljev, 1924). Secretions from a cement gland form a cuticle over the egg with a stalk at one side, a process that takes about two hours (John, 1933). The eggs, about 0.3 mm in size and enclosed in a thin transparent membrane, are laid, according to John (1933), at low tide to protect them from strong current of the receding waters. Ghirardelli (1968) states laying may happen at any time but Vasilijev (1924) thinks the nights are preferred. In *Eukrohnia bathyantarctica,* eggs are laid into incubatory pouches (also called ‘brood sacs’ or ‘marsupial sacs’) at the vaginal opening to the exterior, where the eggs are protected during development. The pouches are also ventrally protected by the bending over of the laminar part of the lateral fins (Fig. 2).

Sanzo (1937) notes the eggs of *Pterosagitta draco* are clumped in a gelatinous oötheca (6.00 mm × 6.04 mm) containing about 200 eggs. I have found these oöthecae, 7.0 mm × 5.8 mm, in plankton samples from California, but with fewer eggs (approximately 50). The jelly substance from which the oötheca is built is apparently produced by the vaginal glands. The oötheca sinks slowly, protecting the eggs from the action of waves, sudden changes in both temperature and salinity, and from predation.

Sagitta hispida eggs are extruded, covered by layers of gelatinous substance, in two linear rows (Conant, 1896) but occasionally may be separated. They do not float and are submerged in the waters. Egg clumps of *S. hispida* and *S. helenae* appear stuck to the wall of the aquaria (Reeve and Lester, 1974; Reeve and Cosper, 1975), merely because of the meniscal physical surface tension. The exact time of laying of eggs appears to depend on temperature, about early in the morning in July but later on during cold days.

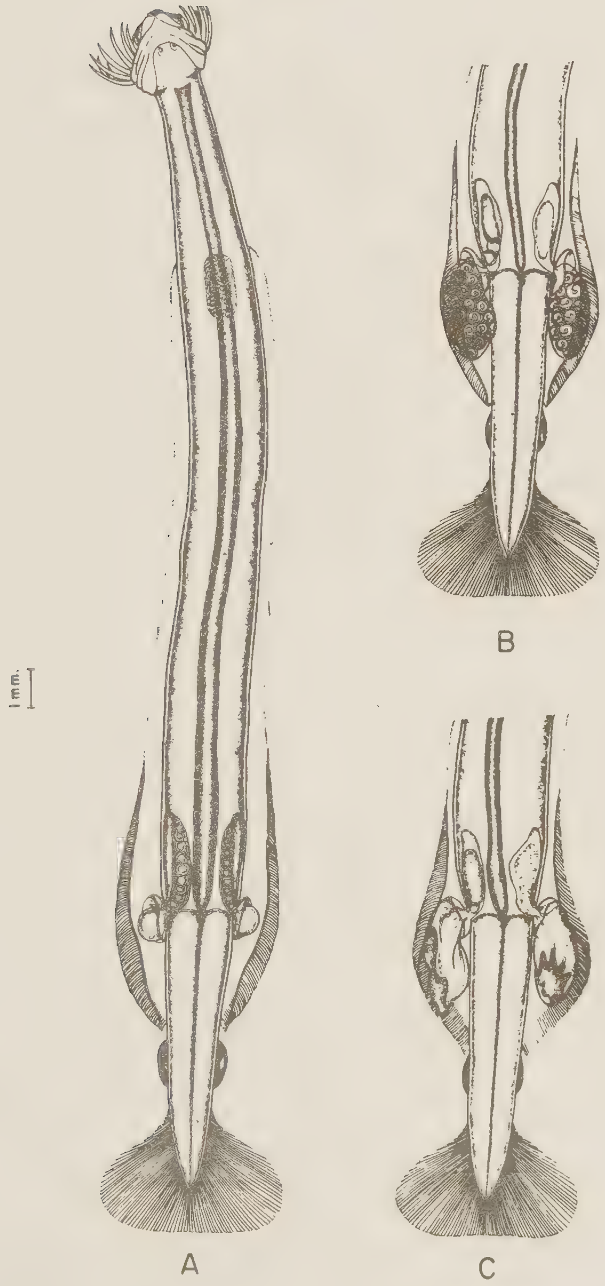

Fig. 2. *Eukrohnia bathyantarctica.* **A**: Complete animal (dorsal view) with incipient marsupial (brood) sacs at the vaginal opening to the exterior. **B**: Marsupial sacs filled with eggs containing embryos in a single coil (Stage III; dorsal view). **C**: Marsupial sacs broken (dorsal view). (From Alvariño, 1968.)

V. DEVELOPMENT

A. Cleavage and Embryonic Development

Cleavage is regular in *Spadella* and *Sagitta* species, where the yolk is uniformly distributed throughout the egg. When a great amount of yolk is present, segmentation is irregular and incomplete, as the yolk generally tends to get concentrated at the vegetal pole of the egg and interferes with the division of the protoplasm at this pole. As a result, the animal pole segments rapidly and the vegetal pole only slowly.

The first few cleavages produce a spherical blastula, with a well-marked blastocoel. The blastomeres are equal and opaque. In *Sagitta,* the blastocoel appears at the 8-cell stage itself, but not in *Spadella* in which the eight-cell-stage embryo is still solid with no trace of a blastocoel (John, 1933). Cleavage proceeds rapidly during the next two divisions. Six hours after laying of the egg, one side of the blastula flattens and invaginates into the blastocoelic cavity. At the end of seven hours, the embryo is a typical gastrula comprising two layers, an outer epiblast and an inner hypoblast. The latter encloses a wide space, the archenteric cavity which opens out by a narrow blastopore at one end. When the embryo is 14-hours old, three areas of the archenteric cavity are clearly seen : germ cells in the middle part of the anterior region, surrounded on either side by the archenteric folds. Some hours later, the two germ cells divide to form four cells, one pair to the right and the other pair to the left of the median line (see Fig. 3).

When the embryo is about 24-hours old, the posterior ends of the two archenteric folds come into contact with each other occluding the opening; the intestine now becomes a closed tube with a narrow lumen, and begins to elongate. The coelomic pouches are separated into right and left body cavity. A small constriction appears at the anterior end of the coelomic sacs and a small ring of mesoblasts is already present at the anterior end of the embryo at about 27 hours; the head is also outlined. Ganglion cells begin to appear, and the embryo starts to curve inside the egg membrane. The embryo elongates, the head becomes thicker and broader, and the tail tapers. In embryos, 35-hours old, the ganglion cells can be clearly observed which multiply rapidly, and the three regions of the body (head, trunk, and tail) are also distinct (Fig. 3). The embryo hatches at the end of about 48 hours as a young 'larva' which resembles broadly the adult: transition to the adult sate therefore involves no metamorphosis.

B. Hatching

The hatching of eggs is a process under the action of various agents and mechanisms. The egg case may be disintegrated by enzyme action; rupture may be due to osmotic swelling of the embryo, by purely mechanical action, or by movement of the embryo (Barnes, 1955).

The first sign of hatching is a slight vibration of the appendages, seen mainly

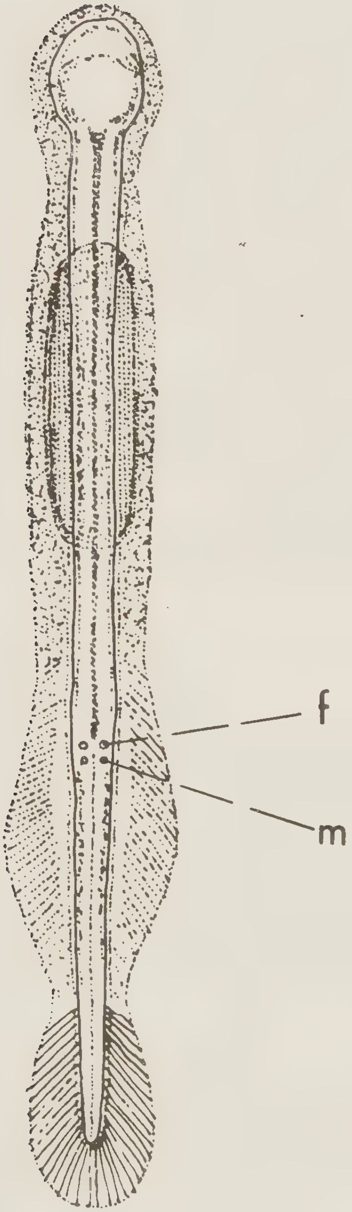

Fig. 3. Diagram of the larva of a chaetognath. The head, trunk and tail are already evident. f, Female germinal cells; m, male germinal cells.

from the ventral side of the embryo. This twitching is first slight but extends later to other parts of the body, resulting in marked flexions of the caudal region and in up-and-down movements of the tail and appendages. The mechanical pressure resulting from these movements produces a distension of the egg case, and eventually leads to its rupture. The larva moves forward by flexions of the caudal sector and usually emerges, head first, with the hooks held close to the sides of the head.

Hatching in *Sagitta enflata* starts with contractions at each end of the embryo, extending to the middle region, producing the effect of uncoiling of the organism, and forcing its tail and head against the egg membrane. The contractions become more pronounced 10 to 15 minutes before hatching, and immediately before hatching, take the form of an uninterrupted series of violent jerking movements.

After hatching, the larvae swim with the same series of darts that characterize the adult chaetognaths. *Spadella* larvae, however, do not swim much; they attach themselves immediately to the substratum by adhesive clusters or palmar devices at the ventral side of their tail.

The two primordial germ cells located in the trunk cavity adjacent to the posterior septum and the other two situated behind are visible soon after hatching. The ovaries develop from the two germ cells in the trunk cavity, and the testes from corresponding cells in the tail cavity.

Immediately after hatching, the alimentary system is relatively undeveloped and the fins are delicate membranes, the whole body being covered by an alveolar epithelium.

C. Larval Development

Development is rapid (at least in warm-water species) at 20° to 30°C. In a few hours the rays of the tail fin are well formed, and those of the posterior part of the lateral fins also appear. The tail fin needs to develop first, as it is the main part in the propulsion system of the animal. In the next few hours, the interstitial tissues of the fins grow progressively from the body wall. the newly hatched animals begin to feed 48 hours after laying of the egg, or within three days.

The 'tangoreceptors', at first few in number, project relatively farther from the body wall, increasing in number while decreasing in relative size to the length of the animal. After several days, the anterior lateral fins in *Sagitta* specimens begin to develop.

Development of *Sagitta crassa* larvae was observed in the laboratory by Murakami (1959, 1966) who noted that lack of adequate food arrested the rate of development.

The major problem in successfully rearing pelagic chaetognaths is the difficulty in obtaining undemaged specimens. Neritic species are better suited for experiments, as they are able to withstand sudden changes in temperature, salinity, and mechanical action than the oceanic species.

Newly hatched two-day-old *Sagitta elegans* larvae (Kotori, 1975) ranged in length from 1.23 mm to 1.42 mm (from the top of the head to the tip of the tail). Only a pair of the lateral fins, a thick collarette covering the body, and a median vertical septum at the posterior part of the body appear at this stage; the tail transverse septum is absent, and the ventral ganglion occupies about half the length of the trunk (i.e. 23 to 33 per cent of the total length). Seven-day-old larvae (1.69 to 2.20 mm long) have eight hooks at each side of the head and no eyes, whereas in specimens, 2.05 mm and 4.93 mm long, the eyes have already appeared. *Sagitta elegans* larvae, 5.10 mm long, generally have well-defined anterior fins, but according to Kotori (1975), some larvae, 5.20 to 6.45 mm long, still lacked independent anterior fins. Metamorphosis from larva to juvenile takes place at these sizes. In specimens 7.90 mm long, the ovaries begin to appear. The seminal vesicles develop in specimens 18.2 mm long, and become fully mature at 23.9 mm.

1. Stages of development of the larvae

Four stages (I to IV) are described here in development of the larvae of chaetognaths, partly after Kotori (1975):– Stage I: newly hatched larvae, up to the phase when transverse septum (tail-trunk) makes its appearance; Stage II: the stage during which head armature is developed, but eye pigment is absent; Stage III: eye pigment is present; Stage IV: the two pairs of lateral fins have been formed (in *Sagitta* species) but the gonad is yet to be developed.

Stage IV in development of the larvae comprises the beginning of the juvenile period; sexual maturation is marked by the appearance of gonads as small round bodies (female) and thin tubes (male).

2. Evolutionary considerations and the larvae

In *Sagitta,* the larval stage comes to an end as the paired anterior lateral fins appear; in other genera, with no anterior fins, that stage is only indicated by proper development of the particular generic characteristics of the lateral fins. Also at this stage, the beginnings of gonad formation are visible. In *Eukrohnia,* with a long pair of lateral fins, initiation of the juvenile stage is marked by separation of the tail fin from the lateral fins.

Larvae of the genus *Eukrohnia* appear to resemble closely their adults, but less so are those of *Krohnitta, Pterosagitta, Heterosagitta,* and *Sagitta*—in that order.

3. Hatching mechanisms

The emergence of a juvenile animal or larva from the egg membrane or shell is an extremely critical period of its life, as the developing animal is sufficiently protected while within the egg from vagaries of environmental conditions, both biotic and abiotic. The young at hatching time need to remove their protecting covering, and may get damaged and exhausted in the process. Once free, the young rely upon alertness, speed of response, and strength for their survival.

In spite of the importance of the process of eclosion in survival to animals, hatching has been little studied, the observations available often being incidental during the study of other problems. Embryologists should study the nature of egg membranes present at the time of oviposition, but no work of this type has been done on Chaetognatha (see Alvariño Volume I). Though the eggs and embryology of chaetognaths have been described by several investigators, only Murakami (1959) deals with hatching and provides photomicrographs of the different states of eclosion. Obviously, a great deal of investigation is needed, both to ascertain hatching mechanisms in many groups and to check the reliability of the incidental observations that have been reported on the subject. Hatching mechanisms are quite varied among aquatic invertebrates. As far as we know, eclosion from the egg may be strictly mechanical, i.e. by the action of egg buster, hooks, or by non-mechanical means. Possible mechanisms of eclosion include: (1) the bursting of the egg membrane by osmotic intake of water; (2) active uptake of water by the embryo itself, producing an internal pressure that would burst open the egg membrane; (3) action of an enzyme produced by the embryo or larvae, which dissolves all or a limited portion of the membrane; (4) parental help in breaking open the shell or in flushing the embryos out of the broken egg membrane; (5) a combination of the various processes mentioned above (see also Section VI).

4. Larval development and behaviour

The embryo of *Spadella* hatches (John, 1933) in about 48 hours as a yound larva. A few hours before hatching, the embryo shows signs of movement inside the egg membrane. At the time of hatching the egg membrane bursts; the larva wriggles out and straightens itself; and with little further effort sinks to the bottom of the container and tries to adhere to a substratum and crawl.

The eggs laid in a cluster may all hatch at the same time or successively; in any case, all the larvae which come out from the same cluster of eggs adhere to their empty egg membranes for some time. When disturbed they detach themselves from the egg membrane, wriggle for a short distance, and settle back in resting position. Transparent new-born larvae remain in schools and do not move much except when disturbed.

Differences in behaviour of the larvae of *Sagitta* and *Spadella* may be traced back to differences in the life of their adults. Young *Sagitta,* for instance, are transparent, almost invisible, and lie motionless near the surface of the waters. Transparency is a useful characteristic for animals and their larvae with predatory tendencies: unseen by other animals, they can attack their prey. When disturbed the larvae of *Sagitta* swim like the adults. On the other hand, the larvae of *Spadella* have the habit of adhering to surfaces and crawling over the substratum; occasionally they also swim. The adhesive abilities of *Spadella* larvae are essential for survival in the *Spadella* habitat. Adhesion is effected by adhesive capsules or palmate structures developed at the posterio-ventral part of the tail. Corona ciliata, which may be of vital importance in survival of the animal, appears during the four-day-long larval development.

VI. BREEDING CHARACTERISTICS AND BROOD CARE

Table 1 summarizes the breeding peculiarities of the various genera of chaetognaths (Alvariño, 1968). Nördgaard (1905) was the first to describe a brood sac or marsupium in *Eukrohnia* collected at the Vest Fjord from 600–300 m depth; subsequently, Ritter-Zahony (1910) confirmed its presence in specimens of *Eukrohnia,* 30 mm long, collected at 900–750 m depth. Alvariño (1968) described the egg sacs in *E. bathyantarctica. Eukrohnia* species appear to be inhabitants mainly of the deep strata of world oceans and polar regions. Temperatures here are similar to those obtaining in the Bay of Fundy and Gulf of St. Lawrence, but in both localities *S. elegans* only lays free eggs and various stages of their development have been observed by Huntsman and Reid (1921). It appears that the eggs of different species of the most evolved genus, *Sagitta,* are better equipped for survival by virtue of the chemical composition of their vitellus (Alvariño, 1968) or by the nature of the involucrum covering the egg.

Table 1

Breeding particularities of different genera of Chaetognatha

Genus	Generic characteristics	Breeding characteristics
Eukrohnia	One pair of lateral fins (from ganglion to tail); one pair of sets of teeth	Brood (egg) sac or marsupium
Krohnitta	One pair of rayed fins from tail to the posterior part of the trunk	Probably as in *Eukrohnia*
Heterokrohnia	One set of paired fins from tail to the level of the ventral ganglion; two pairs of sets of teeth	Unknown
Pterosagitta	One pair of paired fins, from tail to the posterior septum; two sets of teeth	Pelagic jelly oötheca
Sagitta	Two paired lateral fins; two pairs of sets of teeth	Free eggs covered by a thick involucrum

It is well known that Arctic animals brood their eggs or provide some other method of protection of the egg until the embryo develops into a large larva or young animal. In this way the larval period is cut short. On the contrary, species inhabiting temperate, equatorial or tropical waters lay only small eggs that produce small larvae. Large larvae with a short larval period are generally obtained only if the eggs are large or the eggs develop in incubatory folds, sacs, etc. under the protection of the parent. Species of *Eukrohnia* brood the eggs until the young are 3 mm in length (*E. bathyantarctica*: Alvariño, 1968; *E. bathypelagica* identified as *E. hamata:* Dawson, 1968; *E. hamata:* MacGinite, 1955). The sacs are in communication with the respective oviducts by a fine tube.

Alvariño (1967a, 1968) illustrated some pieces of sac-like remnant hanging from the oviduct of *Eukohnia fowleri*, and in 1968 observed specimens of *E. bathyantarctica* from the Antarctic and Subantarctic regions with sacs containing eggs. The brood sacs were of different sizes indicating the eggs within were in different stages of development in different animals. Eggs in the marsupial sac were at different stages of development, ranging from the formation of the blastomeres and various phases of development of the embryos up to the larval stage ready for eclosion. Some sacs were full of larvae already hatched from the eggs. Five stages (I to V) have been distinguished by Alvariño (1968) in the brooding phase:

Stage I : brood sac developing;
Stage II : brood sac filled with eggs developed up to the gastrula stage;
Stage III : brood sac with eggs containing embryos in a single coil;
Stage IV : brood sac with eggs containing double-coiled embryos;
Stage V : brood sac filled with larvae, or broken after the extrusion of the larvae.

According to Ritter-Zahony (1910), brood sacs are not present in the genus *Krohnitta,* but Schilp (1941) noted small membraneous sacs at level with the trunktail septum, in *K. subtilis*. Sanzo (1937) observed the pelagic oötheca of *Pterosagitta draco* containing mature eggs. The gelatinous substance protects both eggs and larvae from the various physico-chemical changes until eclosion. Gelatinous egg clusters measured 6.0 to 6.4 mm in diameter, and the spherical eggs therein 0.40 to 0.46 mm (Figs. 4 and 5).

Species of *Sagitta* lay their eggs free in surface waters (Fig. 6). The eggs are pushed out by ovarian contractions and extruded in two rows, one from each oviduct.

Eclosion and its mechanisms have been briefly described in Section VB and C 3. In many animals, the 'oviducal membrane' is broken by the action of a powerful proteolytic enzyme (protease) reportedly secreted by the embryo at the time of its release (Barnes and Barnes, 1977). In the genus *Eukrohnia* with brood sacs, extracts of the adult could stimulate and synchronize hatching if conditions in the environment are adequate for the survival of the young (presence of phytoplankton and young calanoids).

More information is needed on mechanisms involved in breaking of the membrane of the brood (egg) sacs. The following possibilities may be considered: (1) bacterial activity within the sac cavity; (2) action of some substance released by the adult. If a second cycle of maturity occurs, nutrients will be used for restoration of the gonad and for formation of new gametes, a process that requires a high degree of oxygenation. The egg sac, which receives far too little oxygenation, cannot be sustained and disintegration takes place; (3) action of a substance released by the larvae, or mechanical action of the larvae, eclosed from the egg.

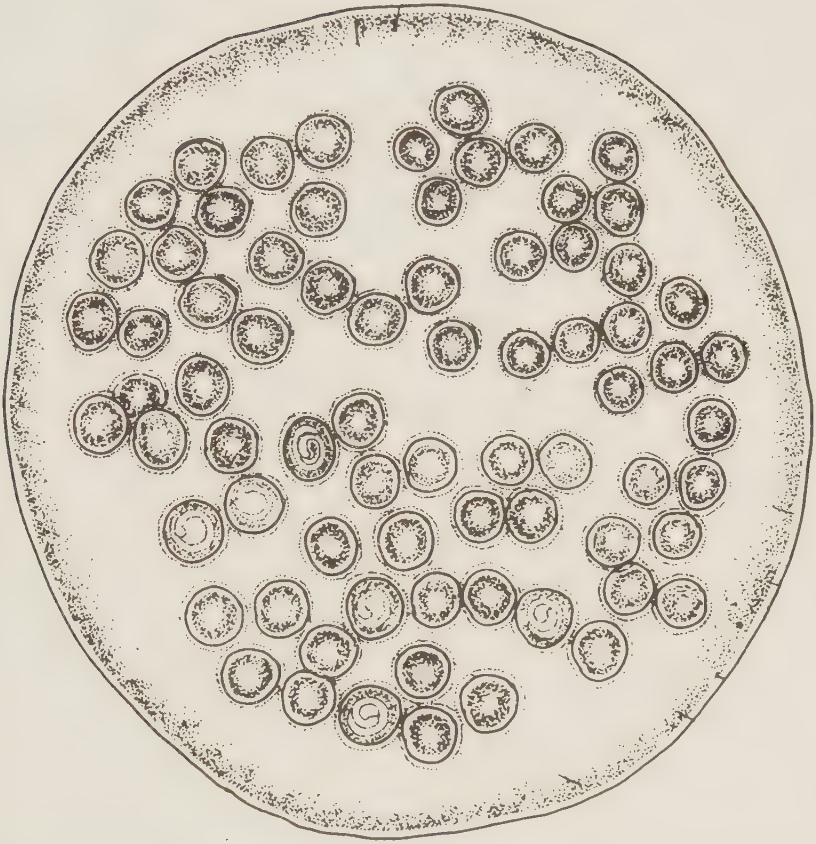

Fig. 4. Jelly oötheca of *Pterosagitta draco*, with eggs at various stages of development up to single-and double-coiled embryos.

Since the breakdown of the brood sac synchronizes with the 'maturity' of the larvae, all the three possibilities may be in action. The larvae may be producing the necessary enzyme(s) to destroy the sac in response to some hatching factor (Barnes, 1957) or stimulation produced by some chemical on the adult; bacterial action may play a part mainly in disintegration of the jelly oöthecae.

VII. SIZE DISTRIBUTION AND BREEDING SEASONS

Environmental factors affecting the breeding seasons are: temperature, illumination, and nutrition. Reproductive phases in many animals are dependent upon corresponding changes in quality and quantity of the food available during their development and life span. The production of plants and the grazing ability of animals are subject to seasonal variations. Most species breed in the spring. Breeding cannot begin earlier than the vernal development of the phytoplankton, the food of small *Calanus*, the primary prey of Chaetognatha.

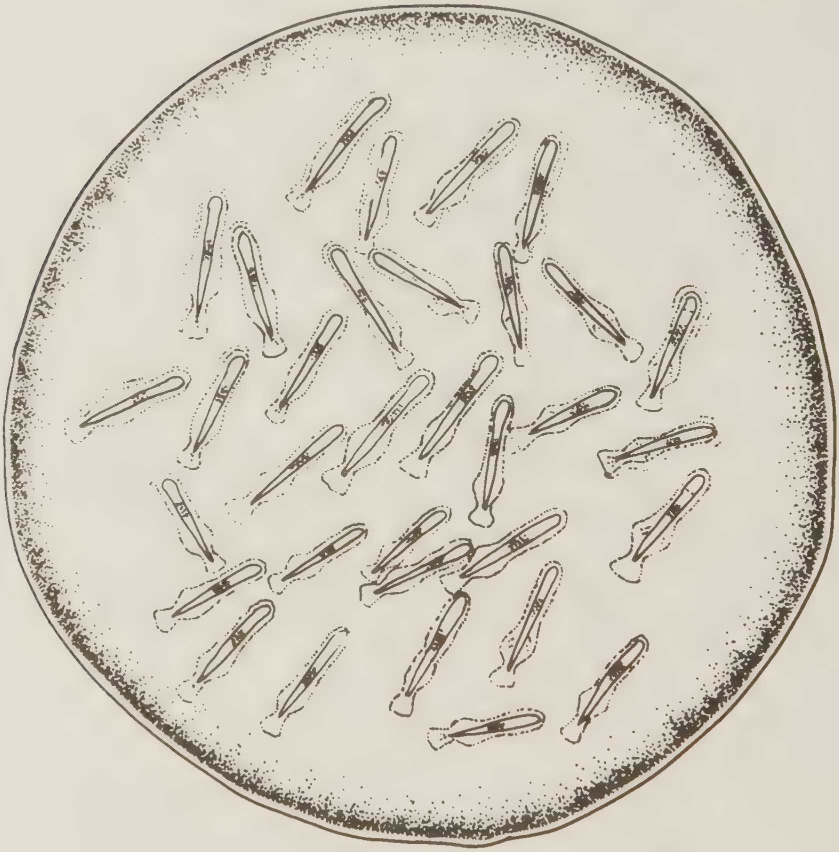

Fig. 5. Jelly oötheca of *Pterosagitta draco,* with hatched larvae.

In species that reproduce all year round, the size of the broods varies with the supply of phytoplankton, on which depend the copepods. However, these variations in carnivorous zooplankters are insignificant when compared with those in herbivorous plankters (population controlled by the predation pressure and food supply). In tropical regions, reproduction is a continuous process along the year.

The breeding season of a species is the period of the year, when most individuals in a population have ripe gametes in abundance, ready to be released, and is usually indicated by months or seasons. In most chaetognaths, there is only one gametogenic cycle in the life of each individual. The gametes may be released all at once, or intermittently during the few days of the season. The extent of the breeding seasons increases from the high to the low latitudes, which is a function of temperature and the quantity and quality of food available. Table 2 indicates the breeding seasons for most species of Chaetognatha, and the regions they inhabit.

Juvenile, immature, and mature individuals all show seasonal trends in their biochemical composition. This indicates that environmental and trophic conditions and changes in gross biochemical composition play a role, more than the seasons

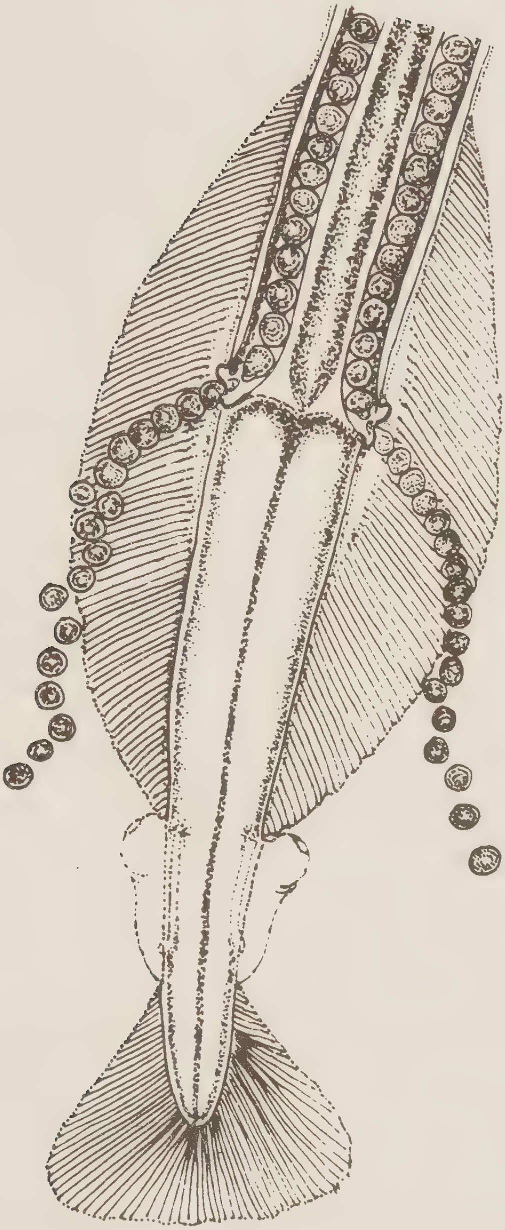

Fig. 6. Free pelagic egg-laying in species of *Sagitta*. The vaginal opening (female sexual pore) is at the dorsal edge on each side.

per se, in determining the breeding cycle. It is not known how the final adaptation timing the cycles, in order that the production of larvae or juveniles is synchronized with periods of favourable feeding, is reached.

Eggs of *Sagitta elegans* were identified in the Bay of Fundy and Gulf of St. Lawrence (Huntsman and Reid, 1921) with double-coiled embryos, in April and

Table 2

Seasons of reproduction of species of Chaetognatha in various oceanic regions

Species	Region	Breeding period	References
Spadella cephaloptera	Marseille	Spring to autumn	Furnestin and Brunet, 1965
	Naples	Spring to autumn	Ghirardelli, 1959
	Roscoff	Spring to autumn	Nouvel, 1935
	Villefranche-Sur-Mer and Naples	All year round, peaks in spring and summer	Vasiljev, 1924
Eukrohnia bathyantarctica	—	—	—
E. bathypelagica	—	—	—
E. fowleri	—	—	—
E. hamata	Greenland	Summer	Kramp, 1939
	Korsfjorden, Norway	April to November	Sands, 1977
E. minuta			
Krohnitta mutabbii	Florida	All year round	Owre, 1960
K. pacifica	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
K. subtilis	California	Spring to summer	Alvariño, 1967b
	Florida	Summer to winter	Owre, 1960
Pterosagitta draco	California	Spring to summer	Alvariño, 1967b
Sagitta bedfordii	Indonesia	All year round	Alvariño, 1965a
S. bedoti	Tropic-equatorial Indo-pacific	All year round	Alvariño, 1965a
S. bierii	California	January to October	Alvariño, 1967b
S. bipunctata	Central Pacific	January to October	Alvariño, 1967b
	Florida	Late winter to early spring	Owre, 1960
S. bombayensis	Eastern India	March to September	Lele and Gae, 1936
S. bruuni	Gulf of Thailand and South China Sea	All year round	Alvariño (unpubl. data)
S. crassa	Seto Inland Sea	Spring, summer, autumn	Murakami, 1959
	Sea of Japan	February to November	Murakami, 1966
	Yellow Sea	March to October	Murakami, 1966
	Chinhae Bay, Korea	March to November	Park, 1970
S. decipiens	California	Spring to autumn	Alvariño, 1967b
	Florida	Summer, winter	Owre, 1960
S. elegans	Gulf of Maine	Spring and summer	Bigelow, 1926
	Martha's Vineyard to Cape Hatteras	Late Winter to early spring	Bigelow and Sears, 1939
	Basents Sea	Summer	Bogorov, 1940
	Georges Bank, Nantucket	April to September	Clarke *et al.*, 1943
	Chesapeake Bay	Late winter to summer	Cowles, 1930
	Delaware	February to May	Deevey, 1960
	Baffin Island, Labrador	June to October	Dunbar, 1941
	Eastern Canadian Arctic	July to December	Dunbar, 1962

Species	Region	Breeding period	References
S. elegans	Woods Hole	March to September	Fish, 1925
	Bering Sea	June to September	Heinrich, 1962
	Eastern Canada	Spring and summer	Huntsman, 1919
	Bay of Fundy, Gulf of St. Lawrence	April to October	Huntsman and Reid, 1921
	Oslofjord	April to September	Jakobsen, 1971
	Greenland	April to September	Kramp, 1917, 1939
	Sagami Bay, Japan	Brought into the area in spring-summer	Marumo, 1966
	North Sea	April to October	Meek, 1928
	Korea	Early spring	Park, 1970
	Irish Sea, Port Erin	January to May	Pierce, 1941
	Gulf of Maine, Georges Bank	Spring and summer	Redfield and Beale, 1940
	Plymouth (Great Britain)	March to September	Russell, 1932a
	St. Margaret's Bay, Nova Scotia	April to September	Sameoto, 1971
	Gulf of Maine	Spring to fall	Sherman and Schaner, 1968
	Eastern Greenland	February to June	Ussing, 1938
	Norwegian Sea	April to May	Wiborg, 1955
	Bedford Basin	Spring to autumn	Zo, 1973
S. enflata	Iberian Atlantic	Most of the year	Alvariño, 1957
	California	All year round	Alvariño, 1967b
	Mediterranean	All year round	Furnestin, 1957
	Miami	March to August, November to January	Owre, 1960
	Kaneohe Bay, Hawaii	All year round	Piyakarnchana, 1965
	Southeast Australia	Most of the year	Thomson, 1947
S. euneritica	California	All year round	Alvariño, 1967b
S. euxina	Roumanian Black Sea	November to May	Elian, 1960
S. ferox	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. friderici	Iberian Atlantic	All year round, peaks in spring-summer	Alvariño (unpubl. data)
S. gazellae	Antarctic-Subantarctic	Spring and summer	Alvariño *et al.*, 1978
	Antarctic-Subantarctic	Late March to autumn	David, 1955
S. helenae	Miami	Spring	Owre, 1960
	Florida	All year round	Pierce, 1951
S. hexaptera	California	Spring-summer	Alvariño, 1967b
	Indonesia	All year round	Schilp, 1941
S. hispida	Miami	April to December	Owre, 1960
	Gulf of Mexico and Florida	All year round	Pierce, 1951

Table 2 (*Contd.*)

Species	Region	Breeding period	References
S. hispida	Biscayne Bay, Florida	November to May	Reeve, 1966
	Biscayne Bay, Florida	All year round except in summer	Reeve and Walter, 1972a,b
S. johorensis	Indonesia	All year round	Alvariño, 1967a
S. lyra	Miami	May to February	Owre, 1960
S. macrocephala			
S. marri			
S. maxima	Greenland, Davis Strait, Uyanak Fjord	Spring and Summer	Kramp, 1917
	Greenland	Summer to autumn	Kramp, 1939
S. minima	California	Spring and summer	Alvariño, 1967b
	Florida	Spring to autumn	Owre, 1960
S. nagae	Suruga Bay	April to September	Nagasawa and Marumo, 1978
S. neglecta	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1967a
S. oceania	Indonesia, S.E. Asia	All year round	Alvariño, 1965a
S. pacifica	California	Spring and summer	Alvariño, 1967b
S. peruviana			
S. planctonis			
S. popovicii			
S. pseudoserratodentata	California	Spring and summer	Alvariño, 1967b
S. pulchra	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. regularis	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. robusta	Tropic-equatorial Indo-Pacific	All year round	Alvariño, 1965a
S. scrippsae	California	Spring to autumn	Alvariño, 1967b
S. septata	Indonesia, S.E. Asia	All year round	Alvariño, 1965a
S. serratodentata	Delaware	Summer to autumn	Deevey, 1960
	Miami	All year round	Owre, 1960
S. setosa	Villefranche-sur-Mer	Spring and summer	Dallot and Palazzoli, 1976
	Roumanian Black Sea	June	Elian, 1960
	Irish Sea, Jersey Channel	April to August	Pierce, 1941
	Plymouth, Great Britain	February to October	Russell, 1932b
	North Sea	March to September	Wimpenny, 1937
S. tasmanica			
S. tenuis	Florida	All year round, except probably October	Pierce, 1951
S. tokiokai			
S. zetesios	West Greenland	May	Kramp, 1917

May, but disappeared in the middle of June. Their Stage I eggs (up to gastrula) decreased progressively and Stage III (double-coiled embryos) increased until the eggs all disappeared. Small *S. elegans*, 2 mm long, appeared at the end of May and were still found up to the middle of June; by July the smallest were 7 mm long. The sudden disappearance of the eggs in June coincided with an abrupt decrease in the number of adults in plankton hauls. The breeding season of *S. elegans* in the Bay of Fundy (Huntsman and Reid, 1921) appears to be long in so far as eggs have been found in the plankton from April to October. Stages I and II eggs (gastrula to single-coiled embryo) seem to be equally abundant at surface and at 5–7 m depth. There is some indication that Stage III eggs (double-coiled embryo) reach deeper layers than those sampled. The young are more widely distributed in the Bay of Fundy than the adults, and more abundant in the estuaries than in the open Bay.

Sagitta elegans spawns over a long period in the Canadian Eastern Arctic (Dunbar, 1962), from July into winter, probably February. Winter breeding implies that this process is not timed to coincide with maximum abundance of food; the cycle is determined by growth limitations imposed by low temperature that slows down metabolism. In Korean waters, the size composition of *S. elegans* in larger in winter than in other seasons, the mature individuals constituting as much as 40 per cent of the samples (Park, 1970). The main period of reproduction is early spring. *S. elegans* begins to breed early in St. Margaret's Bay, Nova Scotia (Sameoto, 1971). The first eggs appear in the samples in May, and the maximum size of the animals decreases from 32 mm to 30 mm in April. The reduction in length is due to breeding and brooding activities of the large animals: the laying of eggs continues into late July.

Table 3 from Sameoto (1971) gives useful data on spawning and maturity and

Table 3

Relationship between life span and mean ambient temperature in *Sagitta elegans* (modified from Sameoto, 1971)

Date of birth	Date of maturity	Life span in days	Mean water temperature	Degree/days*
7 October 1968	1 May 1969	206	4.2°C	865
25 October 1968	15 May 1969	200	3.8	760
25 November 1968	1 July 1969	219	3.6	788
15 December 1968	15 July 1969	213	3.5	745
15 April 1969	1 September 1969	142	5.2	738
1 May 1969	15 September 1969	137	6.1	866
15 May 1969	9 October 1969	147	6.8	1000
1 July 1969	25 October 1969	115	7.4	851
15 July 1969	26 November 1969	133	8.1	1077
1 September 1969	5 December 1969	95	9.0	855
15 September 1969	12 December 1969	91	9.1	822**

*Total temperature the animal has been exposed to during the life span;

**See text for discussion.

the relationship between the length of the life span and temperature of the waters in *Sagitta elegans*. It may be noted that the population born on 15 September 1969 and exposed to 822 degree/days, matured by 12 December 1969 and ceased to grow further; some of their offspring in fact could receive only 549 degree/days (Sameoto, 1971). Therefore, this overwintered population had not matured and it was the first to breed in 1970. This provided the clue to determine the minimum degree/days needed by *S. elegans* to reach maturity. Low mean temperatures, during the development of the animals, increased the length of the growing period and the time to reach maturity (Table 3).

Several chaetognaths, including, *Sagitta elegans,* have been long used as indicator organisms of water masses (Russell, 1932 a,b, 1936; Alvariño, 1965 a, b). The knowledge that *S. elegans* needs a minimum of 738 degree/days to reach gonad maturity (Table 3) is used as a base to calculate the length of the life cycle as a function of mean water temperature. The length obtained at maturity and the time of breeding of *S. elegans* will provide a useful clue to the temperature of the waters inhabited by it and in identifying the water masses in which it originates (Sameoto, 1971).

VIII. SUCCESS OF REPRODUCTION AND GROWTH

However, in these estimations (Section VII), the kind of food and their availability were not considered. Long-term studies have shown that a relationship exists between the size of the copepod (or other prey) population and that of *Sagitta elegans* population. In coastal waters of the Gulf of Maine (Sherman and Schaner, 1968), this species has a prolonged period of breeding, from late spring through the autumn. The abundance of specimens at Stages I and II of maturity suggested that no significant breeding occurred in winter. *S. elegans* in this region has only one breeding period per year.

The number of generations produced in a year obviously varies with the species, but is also correlated with the environment. Generally, the number of generations produced by a species in a year, increases with the distance from the poles (Owre, 1960). Thus *Sagitta elegans* (Ussing, 1938; Kramp, 1939; Alvariño, 1965a) reproduces once a year in the Arctic and Subarctic regions. *S. gazellae* also breeds likewise only once a year (David, 1955) with abundant reproduction in spring (Alvariño *et al.*, 1978). *S. elegans,* however, reproduces two or five times a year in the north Atlantic while at Port Erin (Pierce, 1941) only once from January to May. In the North Sea (Wimpenny, 1937) and off Nantucket and Georges Bank, there are two breeding periods, one in spring and the other in autumn (Clarke *et al.*, 1943). Differences in length among specimens in fully mature stages have been related to variations in temperature in the course of the year, the longest individuals being found in the colder periods.

The life cycle of *Sagitta elegans* off Plymouth, according to Russell (1932 a,b, 1933 a,b), is completed in 43 days, based on which he suggests five generations could exist each year in the waters of south England. The reproductive cycle of *S. elegans* in the eastern Canadian Arctic has been studied by Dunbar (1941, 1962), who observed that this species has a life span of two years. The spawning period is long, lasting from July into autumn and winter. The breeding cycle is two-phased or alternating in the species population, such that three size-structure populations appear together during the breeding seasons. The smallest may be the offspring of the largest; the intermediate-size population (adolescent group), born the previous year (one-year old), will breed the following year (Dunbar, 1962). The breeding cycle is determined by the slow growth rate at low temperature, to which there has been no adaptation. The young are born during a period of maximum abundance of food.

Hydrographical differences, though not great, are nevertheless reflected in the biology of *Sagitta elegans* from the Arctic and Atlantic waters. This seems to be of some importance in deciding the timing of sexual maturity. In the specialized environment of Ogac Lake, which is warmer than the proper Arctic, the growth rate is rapid and the breeding cycle single-phased; or it could be alternating as in cold waters. In any case, maturity is reached at half the body length required for cold-water animals (Dunbar, 1962).

Environmental factors also have a great influence on the size of the individuals and their life span. In extreme cold waters, for instance, zooplankton organisms only develop slowly, but reach a large size, and live longer than related species in warm waters (McLaren, 1966). It is believed that generation length in the Arctic is determined by marked seasonality of food supply, corresponding to high fecundity, large size of the individuals, and slow development.

Sagitta gazellae, an Antarctic-Subantarctic chaetognath, grows 5 mm per month (David, 1955) during winter and spring, but faster in summer. The life cycle appears to last one year, and the animal reaches 60 mm in 10 or 11 months (David, 1955). In this connexion, a comparison of the length at which sexual maturity is attained by *Sagitta* species in the Arctic and Antarctic regions would be of interest. *S. elegans* from the Arctic reaches maturity in two years at a length of 30 mm, whereas *S. gazellae* from the Antarctic region does so in one year at length of 90 mm. If these data are reliable, the reported difference between the two regions may be related (to species differences apart) to differences in the quality of food supply and to the quantity and quality of hormones and trace elements favouring accelerated development and growth. This could be put to better test by studying the development of populations *Eukrohnia hamata,* a species common to the Arctic and Antarctic. In Korsfjorden (Norway), *E. hamata* reaches its maximum length during the first year of its life (Sands, 1977), and sexual maturity develops during the second year. The positive correlation between weight and lipid proportion, found for autumn and spring populations, reflects the differences in lipid content between the juveniles and the slow-growing maturing animals. *E. hamata* breeds from spring to the end of autumn in Korsfjorden, with peaks in May and October–November (Sands, 1977).

Sagitta crassa, in the Sea of Japan, has three alternating main breeding periods: February–March, May–July, November–December. The period from laying of eggs to hatching changes with water temperature and chlorinity. A minimum of 15 hours was recorded at temperatures above 27°C and an optimum chlorinity of 17–18 per cent salinity of 31–33%. This species breeds in Chinhae Bay, Korea from March to April and from July to October–November (Park, 1970). In the Yellow Sea, breeding occurs during May–October, especially in July and August. Several generations of *S. crassa* show phenotypic variations: for instance, type C with large collarette is adapted to sudden changes in temperature and salinity, type N (with collarette mainly at neck) prefers waters of high temperature, and type I is intermediate in nature (Murakami, 1966). In Biscayne Bay, Florida, *Sagitta hispida* presents only one breeding season extending from November to March; this is followed by a period of summer inactivity; a period of rapid growth and maturity starts again in the new generations (Reeve, 1966). In species with only one maturity cycle, mixed populations are common due to flow of recruits from other areas. Fluctuations in *S. hispida* populations appear to be related to fluctuations in abundance of food: when the number of adult copepods increases in October, the population of *S. hispida* shows a significant gain in size, maturity, and abundance.

Sagitta enflata exhibits marked polymorphism in relation to stages of maturity and size (Alvariño, 1963a; Piyakarnchana, 1965). Furnestin (1975) thinks two cycles of maturity may occur in the Mediterranean populations; in tropical Atlantic, three or four could be attained. In the Indian Ocean, Rao and Kelly (1962) observed variations in size of this species during the year, larger sizes coinciding with abundance of copepods. In the Agulhas Current, specimens of *S. enflata* from neritic waters generally contained more ova than from oceanic waters (Stone, 1966). This difference may be advantageous in producing sufficient reproductive potential in maintaining populations over a wide range of variations in physical and biological parameters.

Spadella cephaloptera reaches maturity in two months, and it is uncertain if specimens born in autumn overwinter, retiring to the bottom (Ghirardelli, 1959, 1960, 1963). Furnestin and Brunet (1965) at Marseille, Nouvel (1935) at Roscoff, and John (1933) at Plymouth, have confirmed that *Spadella* lie concealed in the bottom silt during the winter months, and that the ones collected in winter are smaller than those collected in spring. *Spadella* living in the prairies of Posidonia show a direct correlation between body growth and number of ova, and the environmental conditions. In both spring and summer, the populations grow fast by producing a large number of eggs

REFERENCES

Alvariño, A. (1957). 'Zooplancton del Atlańtico Ibérico. Campaña del ''Xauen'' en el verano de 1954', *Bol. Inst. Español, Ocean.*, **82**, 1–51.

Alvariño, A. (1963). 'Epiplanktonic Chaetognatha of the Sea of Cortes (Quetognatos epiplanctónicos del Mar de Cortés)', *Rev. Soc. Mex. Hist. Nat.*, **24,** 97–203, and *Contrib. Scripps Inst. Oceanogr.*, **34** (1696), 645–752.

Alvariño, A. (1965a). 'Chaetognaths', *Oceanogr. mar. Biol. Ann. Rev.*, **3,** 115–194.

Alvariño, A. (1965b). 'Distributional atlas of Chaetognatha in the California Current Region during the CalCOFI monthly cruises of 1954 and 1958', *Calif. Coop. Oceanic Fish. Invest. Atlas,* **3,** (I–XIII), 1–291.

Alvariño, A. (1967a). 'The Chaetognatha of the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand. Part I. Systematics', *Scientific Results Mar. Invest. South China Sea and the Gulf* of Thailand, **4**(2), 1–197.

Alvariño, A. (1967b). 'Zoogeography of California: Chaetognatha (Zoogeografia de California: Quetognatos)', *Rev. Soc. Mex Hist. Nat.*, **27,** 199–243, and *Contrib. Scripps Inst. Oceanogr.*, **37**(2139), 487–531.

Alvariño, A. (1968). 'Egg pouches and other reproductive structures in pelagic Chaetognatha', *Pac. Sci.*, **22**(4), 488–492, and *Contrib. Scripps Inst. Oceanogr.*, **38**(2349), 554–558.

Alvariño, A., Hosmer, S.C., and Ford, R.F. (1978). 'Antarctic Chaetognatha', U.S. Antarctic Res. Prog., Eltanin Cruises 20–28, 1965–1967, *Rep. Smith. Ocean. Sorting Center*, pp. 1–107.

Barnes, H. (1955). 'The hatching process in some barnacles', *Oikos*, **6**(2), 114–123.

Barnes, H. (1957). 'Processes of restoration of synchronization in marine ecology: the spring diatom increases and the "spawning" of the common barnacle, *Balanus balanoides* (L)', *Ann. Biol.*, **33,** 67–85.

Barnes, H., and Barnes, M. (1977). 'Studies on the reproduction of cirripeds. II. Setting of the lamellae, action of protease and disintegration of the oviducal sac', *J. exp. mar. Biol. Ecol.*, **27,** 219–231.

Bigelow, H.B. (1926). 'Plankton of the offshore waters of the Gulf of Maine', *Bull. Bur. Fish. Washington,* **40**(2) (Doc. 968), 1–509.

Bigelow, H.B., and Sears, M. (1939). 'Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton', *Mem. Mus. Comp. Zool. Harvard College,* **54,** 189–373.

Bogorov, B.G. (1940). 'On the biology of Euphausiidae and Chaetognatha in the Barents Sea', *Bull. Soc. Naturalists Moscow (Biol.),* **49**(2), 3–18.

Clarke, G.L., Pierce, E.L., and Bumpus, D.F. (1943). 'The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to the hydrographical conditions', *Biol. Bull.*, **85,** 201–226.

Conant, F.S. (1896). 'Notes on the Chaetognaths', *Johns Hopkins Univ. Circ.*, **15**(126), 82–85.

Cowles, R.P. (1930). 'A biological study of the offshore waters of Chesapeake Bay', *Bull. Bur. Fish. Washington,* **46,** 277–381.

Dallot, S., and Palazzoli, S. (1976). 'La production d' oefs du chaetognathe planctonique *Sagitta setosa.* Un example d'estimation pondérale in situ', *Rapp. Proc-Vérb. Comm. Int. Explor. Scient. Mer. Médit.*, **23**(9), 65.

David, P.M. (1955). 'The distribution of *Sagitta gasellae* Ritter-Zahony', *Discovery Rept.*, **27,** 235–278.

Dawson, J.K. (1968). 'Chaetognaths from the Arctic ocean, including the description of a new species of *Heterokrohnia*', *Bull. Southern California Acad. Sci.*, **67**(2), 112–124.

Deevey, G. (1960). 'Plankton Studies', *Bull. Bingham Ocean. Collect. Peabody Mus. Nat. Hist., Yale,* **17**(2), 1–86.

Dunbar, M.J. (1941). 'The breeding cycle in *Sagitta elegans arctica* Aurivillius', *Can. J. Res.*, **19D,** 258–266.

Dunbar, M.J. (1962). 'The life cycle of *Sagitta elegans* in Arctic and Subarctic seas and the modifying effects of hydrographic differences in the environment', *J. Mar. Res.*, **20,** 76–91.

Elian, L. (1960). 'Observations systématiques et biologiques sur les chaetognathes qui se trouvent dans les eaux roumaines de la mer Noire', *Rapp. Proc-Veŕbaux Comm. Int. Explor. Scient. Mer. Médit.*, **15**(2), 359–366.

Fish, C.J. (1925). 'Seasonal distribution of the Woods Hole region', *U.S. Fish. Bull.*, **41** (Doc. 975), 91–179.

Furnestin, M.L. (1957). 'Chaetognathes et zooplancton de secteur Atlantique Marocain', Thesis, Faculty of Science, University of Paris, pp. 1–356.

Furnestin, M.L., and Brunet, M. (1965). 'Sur une station à *Spadella cephaloptera* dans le Golfe de Marseille', *Rapp. Proc-Vérbeaux Comm. Int. Explor. Scient. Mer. Médit.*, **18**(2), 445–450.

Ghirardelli, E. (1959). 'Habitat e biologia della reproduzione nei Chetognati', *Arch. Oceanogr. Limnol.*, *11*(3), 1–18.

Ghirardelli, E. (1960). 'Habitat e biologia della reproduzione nei Chetognati', *Rapp. Proc-Vérbaux Comm. Int. Explor. Scient. Mer. Médit.*, **15**(2), 347–358.

Ghirardelli, E. (1963). 'Stades dématurité sexuelle chez les Chaetognathes, observations préliminaires sur *Spadella cephaloptera*', *Rapp. Proc-Vérbaux Comm. Int. Explor. Scient. Mer. Médit.*, **17**(2), 621–626.

Ghirardelli, E. (1968). 'Some aspects of the biology of the chaetognaths', *Adv. Mar. Biol.*, **6,** 271–375.

Ghiselin, M.T. (1969). 'The evolution of hermaphroditism among animals', *Q. Rev. Biol.*, **44,** 189–208.

Huntsman, A.G. (1919). 'Some quantitative and qualitative plankton studies of the Eastern Canadian plankton. 3. A special study of the Canadian Chaetognatha, their distribution, etc. in the waters of the eastern coast', *Can. Fish. Exped. 1914–1915, Ottawa,* pp. 421–485.

Huntsman, A.G., and Reid, M.E. (1921). 'The success of reproduction in *Sagitta elegans* in the Bay of Fundy and the Gulf of St. Lawrence', *Trans. Roy. Can. Inst.*, **13**(2), 99–112.

Jakobsen, T. (1971). 'On the biology of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in Inner Oslofjord', *Norwegian J. Zool.*, **19**(2), 201–225.

John, G. (1933). 'Habits, structure and development of *Spadella cephaloptera*', *Q. Jl microsc. Sci.*, **75,** 625–696.

Kotori, M. (1975). 'Newly hatched larvae of *Sagitta elegans*', *Bull. Plankton Soc. Jap.*, **21,** 113–114.

Kramp, P.L. (1917). 'Chaetognatha collected by the Tjalfe Expedition to the West Coast of Greenland in 1908 and 1909', *Vid. Medd. Dansk Naturh. Foren.*, **69,** 17–55.

Kramp, P.L. (1939). 'The Godthaab Expedition 1928, Chaetognatha', *Medd. Grønland Komm. Vid. unders. Grønland,* **80**(5), 1–38.

Lele, S.H., and Gae, P.B. (1936). 'Common *Sagittae* of the Bombay Harbour', *J. Univ. Bombay,* **4**(5), 105–113.

MacGinite, G.E. (1955). 'Distribution and ecology of the marine invertebrates of Point Barrow, Alaska', *Smith. Misc. Coll.*, **128**(9), 1–21.

Marumo, R. (1966). '*Sagitta elegans* in Oyashio undercurrent', *J. Oceanogr. Soc Jap.*, **22**(4), 129–137.

McLaren, Ian A. (1966). 'Adaptive significance of large size and long life of the chaetognath *Sagitta elegans* in the Arctic', *Ecology,* **47,** 852–855.

Meek, A. (1928). 'On *Sagitta elegans* and *Sagitta setosa* from the Northumbrian plankton with a note on the trematode parasite', *Proc. Zool. Soc. (Lond.),* **29,** 743–776.

Murakami, A. (1959). 'Marine biological study on the planktonic chaetognaths in the Seto Inland Sea', *Bull. Naikai Reg. Fish. Res. Lab.*, **12,** 1–186.

Murakami, A. (1966). 'Rearing experiments of a chaetognath, *Sagitta crassa*', *Inform. Bull. Planktol. Japan,* **13,** 62–65.

Nagasawa, S., and Marumo, R. (1978). 'Reproduction and life history of the chaetognath *Sagitta nagae* Alvariño in Suruga Bay', *Plankton Soc. Japan, Bull.*, **25,** 67–84.

Nördgaard, O. (1905). 'Hydrographical and biological investigations in Norwegian fjords', *Bergens. Mus. Skrifter,* **7**(11A), 23–48.

Nouvel, H. (1935). 'Notes sur la fauna marine de la region de Roscoff', *Trav. Stat. Biol. Roscoff,* **13,** 216–218.

Owre, J.H. (1960). 'Plankton of the Florida current. Part VI. The Chaetognatha', *Bull. mar. Sci. Gulf Carib.*, **10,** 255–322.

Park, J.S. (1970). 'The Chaetognaths of Korean waters', *Bull. Fish. Res. Develop. Agency,* **6,** 1–174.

Pierce, E.L. (1941). 'The occurrence and breeding of *Sagitta elegans* Verrill and *Sagitta setosa* J. Muller in parts of the Irish Sea , *J. mar. biol. Ass. U.K.*, **25,** 113–124.

Pierce, E.L. (1951). 'The Chaetognatha of the West Coast of Florida', *Biol. Bull.*, **100**(3), 206–228.

Piyakarnchana, T. (1975). 'The plankton community in the Southern part of Kaneohe Bay, Oahu, with the special emphasis on the distribution, breeding season and population', Ph. D. thesis, University of Hawaii, pp. 1–193.

Rao, S.T.S., and Kelly, S. (1962). 'Studies on the Chaetognatha of the Indian Seas. Part VI: some remarks on *Sagitta bombayensis* Lele and Gae, 1936', *J. zool. Soc. India*, **14**(2), 226–229.

Redfield, A.C., and Beale, A. (1940). 'Factors determining the distribution of populations of chaetognaths in the Gulf of Maine', *Biol. Bull.*, **79**, 459–487.

Reeve, M.R. (1966). 'Observations on the biology of a chaetognath', in *Some Contemporary Studies in Marine Science* (Ed. H. Barnes), George Allen and Unwin, London, pp. 613–630.

Reeve, M.R. (1970a). 'The biology of Chaetognatha. I. Quantitative aspects of growth and egg production in *Sagitta hispida'*, in *Marine Food Chains* (Ed. J.H. Steele), Oliver and Boyd, Edinburgh, pp. 168–189.

Reeve, M.R. (1970b). 'Complete cycle of development of a pelagic chaetognath in culture', *Nature, Lond.*, **227**, 381.

Reeve, M.R., and Cosper, T.C. (1975). 'Chaetognatha', in *Reproduction of Marine Invertebrates*, Vol. II, *Entoprocts and lesser Coelomates* (Eds. A. C. Giese and J. S. Pearse), Academic Press, New York, pp. 157–181.

Reeve, M.R., and Lester, B. (1974). 'The process of egg-laying in the chaetognath *Sagitta hispida'*, *Biol. Bull.*, **147**, 247–256.

Reeve, M.R., and Walter, M.A. (1972a). 'Conditions of culture, food size selection and the effects of temperature and salinity on growth rate and generation time in *Sagitta hispida* Conant', *J. exp. mar. Biol. Ecol.*, **9**, 191–200.

Reeve, M.R., and Walter, M.A. (1972b). 'Observations and experiments on methods of fertilization in the chaetognath *Sagitta hispida'*, *Biol. Bull.*, **143**, 207–214.

Ritter-Zahony, R. (1910)., 'Die Chatognathen', *Fauna Arctica*, **5**(1), 249–288.

Russell, F.S. (1932a). 'On the biology of *Sagitta*. The breeding and growth of *Sagitta elegans* Verrill in the Plymouth Area', *J. mar. biol. Ass. U.K.*, **18**, 131–145.

Russell, F.S. (1932b). 'On the biology of *Sagitta*. II. The breeding and growth of *Sagitta setosa* J. Muller in the Plymouth area, 1930–31, with a comparison with that of *S. elegans* Verrill', *J. mar. biol. Ass. U.K.*, **18**, 147–160.

Russell, F.S. (1933a). 'On the biology of *Sagitta*. III. A further observation on the growth and breeding of *Sagitta setosa* in the Plymouth area', *J. mar. biol. Ass. U.K.*, **18**, 155–158.

Russell, F.S. (1933b). 'On the biology of *Sagitta*. IV. Observations on the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Muller in the Plymouth area', *J. mar. biol. Ass. U.K.*, **18**, 559–574.

Russell, F.S. (1936). 'A review of some aspects of plankton research', *Rapp. Proc. Verb. Cons. Perm. Intern. Explor. Mer.*, **95**, 5–30.

Sameoto, D.D. (1971). 'Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia', *J. Fish. Res. Board, Can.*, **28**(7), 971–985.

Sands, N.J. (1977). 'Quantitative studies of the chaetognaths from Korsfjorden, Norway', M.S. thesis, University of Washington, Seattle, 102pp.

Sanzo, L. (1937). 'Colonia pelagica di uova di Chetognati (*Spadella draco* Krohn)', *Mem, Regio Comitato Talassogr.* **239**, 1–6.

Schilp, H. (1941). 'Biological results of the SNELLIUS Expedition. The Chaetognatha', *Temminckia*, **6**, 1–99.

Sherman, K., and Schaner, E.G. (1968). 'Observations on the distribution and breeding of *Sagitta elegans* (Chaetognatha) in the coastal waters of the Gulf of Maine', *Limnol. Oceanogr.*, **13**, 618–625.

Stone, J.H. (1966). 'The distribution and fecundity of *Sagitta enflata* Grassi in the Agulhas Current', *J. Anim. Ecol.*, **35**, 533–541.

Thomson, J.M. (1947). 'The chaetognath of southeastern Australia', *Bull. Coun. sci. indus. Res. Melbourne,* **222,** 1–43.

Ussing, H.M. (1938). 'Biology of some important plankton animals in fjords of East Greenland', *Meddr. Grønland,* **100**(7), 1–108.

Vasiljev, A. (1924). Ĺa fécondation chez *Spadella cephaloptera* Lgrhs. et l'origine du corps déterminant la voie germinative', *Biol. Gen.*, **1,** 249–278.

Wiborg, K.F. (1955). 'Zooplankton in relation to hydrography in the Norwegian Sea', *Fisk. Dir. Skr., Ser Havunders,* **11,** 5–56.

Wimpenny, R.S. (1937). 'Distribution, breeding and feeding of some important plankton organisms of southwest North Sea in 1934. *Calanus finmarchius* (Gunn), *Sagitta setosa* (J. Muller) and *Sagitta elegans* (Verrill)', *Fish. Invest. London, Ser.* 2, **215**(3), 1–53.

Zo, Z. (1973). 'Breeding and growth of the chaetognath *Sagitta elegans* in Bedford Basin', *Limnol. Oceanogr.*, **18,** 750–756.

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22. CHAETOGNATHA

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I. INTRODUCTION

The Chaetognatha are marine, highly predaceous carnivorous animals of mostly planktonic habits; their life span and anatomy appear to be devoted to the objective of providing another generation to be born as the parents of most species die soon after reproduction. The body of chaetognaths includes the head, trunk (intestine and ovaries), and tail (testes). They are protandrically hermaphrodite, male gonads maturing earlier than female gonads. Copulation occurs, and spermatozoa are reciprocally transferred to the seminal receptacle of the partner. In this process, they act as functional males, and during the extrusion of the ova into the uterus and vaginal cavity, they act as functional females. Thus in chaetognaths, the sexes are separated in time and location within the body: the trunk segment is female, the tail segment male.

II. HERMAPHRODITISM

Hermaphroditism is a mechanism to ensure fertilization, and to produce new generations in low-density populations, where meeting of partners is infrequent. This is, however, not the case with most species of chaetognaths: in population abundance in the plankton, they are only second to copepods. Hermaphroditism may nevertheless be advantageous to the scanty deep-water populations of chaetognaths. Phylogenetic studies indicate that the oldest genera and species (Alvariño, 1965a, 1968) of chaetognaths include populations of low density. This could be interpreted as a sign that original populations of chaetognaths were small, and that hermaphroditism is an atavic characteristic.

In animals that devote their life exclusively to reproduction, the entire biomass is used to meet this aim. The superb constitution of the ova will ensure the success of reproduction. Hermaphroditic chaetognaths are protandric because the formation and production of male gametes appear to consume far less energy than ovarian maturation. Once male gonads have matured, the animal restores the system and expends all energies for the maturation of the ova, and most die of exhaustion after egg-laying.

III. SEXUAL MATURATION

Segregation of male and female germinal lines in chaetognaths begins in the egg itself (see Alvariño, Volume I, pp. 592–593). Although several authors use the term 'egg' to indicate the female reproductive cell, I like to refer to it as 'ovum'; the term 'egg' will be reserved for fecundated ovum or zygote (Alvariño, 1965a).

A. Classification of Maturity Stages

Several schemes for the classification of developmental stages of chaetognaths have been published (e.g. Kramp, 1917, 1939; Russell, 1932a, b; Thomson, 1947; David, 1955). As sexual maturity is a continuous process, its division into stages is to some extent subjective. Colman (1959) divided development into six stages:

Stage 0: Testes and ovaries are not visible under × 1,000 magnification.
Stage I: Testes are visible, but no spermatogonia or spermatozoa are present in the tail coelom. Ovaries are visible, but very small.
Stage II: Testes fill the tail cavity; spermatogonia are present. Ovaries are developing, ova small.
Stage III: Testes are empty; seminal vesicles are full with sperm. Ovaries and ova are well developed.
Stage IV: Testes are empty; seminal vesicles are broken. Ova are fully mature; seminal receptacle is filled with sperm.
Stage V: Spent. Ovaries are reduced to crumbled remnants.

The genus *Eukrohnia* is the only chaetognath in which specimens at Stage V could be found. It is implied that most, if not all, specimens die after egg-laying, as mentioned above (Section II). Species, such as *Sagitta enflata* are considered to go through more than one reproductive cycle in the life span of the individual. The animal grows at each maturity cycle, and no spent or crumbled ovaries are observed, as transition to the next maturity cycle is progressive. The relative duration of the several stages of maturity, speed of transition from one stage to the next, and the relative speed of development of the testes and ovaries vary not only between species but also, to some extent, between individuals of the same species (Colman, 1959). Intermediate stages, such as I–II and II–III, are often observed.

The works of Kramp (1917) and Russell (1932a) have laid the basis for a precise classification of the maturity stages in chaetognaths. They proposed essentially similar divisions using a combination of maturity stages of sperm and ova. The divisions established were adequate for the species studied, and it was found that not all species of chaetognaths developed in the same sequence, and that the degree of protandry was different in different species. A classification base valid for all species, is difficult. The ovaries begin to develop at the same time as the testes, but mature only later. In general, spermatozoa are entirely evacuated from the tail segment before the ova reach maturity. The spermatozoa enter the seminal vesicles, and, by copulation, pass into the seminal receptacle of the partner.

The facile observation of female gonads as indicative of the maturity stage of individuals has led many authors to base maturity classification only on the development of ovaries. An account of the development of the gametes of Chaetognatha, based on a cytological study of *Sagitta enflata*, has been provided by Ghirardelli (1961a, b).

Numerous classifications of maturity stages are found in the literature, and are compiled in Alvariño (1965a). Needless to say, classification of maturity stages should include both female and male gonads and be described for each species. I have been consistently adopting a four-stage scheme of maturity, beginning from Stage I which includes the juvenile animals after the larval stage to the fully mature state (Stage IV). In general, spermatocytes first appear in Stage II, though sometimes a few may occur in Stage I itself. Spermatocytes and spermatozoa fill the testes in tail cavity during the late Stage II and in Stage III. In some species the spermatozoa are extruded before the end of Stage III, but in others they are still present in Stage IV. Stage V of Kramp (1939) and Colman (1959), with spent ovaries, has only (as explained above) been occasionally found in specimens of the genus *Eukrohnia*. Stage O of Colman (1959), juvenile, is included in Stage I.

Alvariño (1963, 1965a, 1967, 1969) has described the maturity cycles in *Sagitta enflata*. Several size-structure populations of this species consistently coexist in time and space in various regions surveyed by the author. It appears that an early life cycle of maturity includes animals mature at 8 to 9 mm, a second at 14 to 16 mm, and a third at 25 to 27 mm. A similar situation of the mixed-structure populations was observed at the southern part of Keneohe Bay, Oahu, Hawaii by Piyakarnchana (1965). The size (i.e. the length) of the animals given here for each species at each stage of maturity is the average in the main distributional region of the species. Obviously differences are found in body size for each stage of maturity: small specimens may appear at Stage IV of maturity, while some larger ones may still be at Stage I, II, or III of maturity. This is evident in specimens collected from the same plankton haul, indicating a mixture of specimens from different source locations in the distributional range of the species. Differences in size of specimens at various stages of maturity may be related to temperature (maturity being reached at smaller sizes in warm waters) or to variations in the quality and quantity of the food supply.

Young specimens of *Krohnitta subtilis* are not usually found in most 1-m net collections probably because the mesh size of nets commonly used is, 0.5 to 0.6 mm, and 0.31 at the cod-end. It is suspected that *K. subtilis* may reach a size close to that of fully mature individuals at an early stage of maturity. In this way, development of this species differs from that of other species, where both maturity and growth processes run parallel, even in species undergoing several maturity cycles. In general, specimens of *K. subtilis*, less than 10 mm long, are juveniles (neither testes nor ovaries are visible). During the last stage of maturity, the seminal vesicles are open, but not broken, and are probably filled more than once during the life cycle (Alvariño, 1967).

Tables 1–28 show the stages of maturity of several species of Chaetognatha (Alvariño, 1962, 1965a, 1967). The four stages of maturity of all species, except *Sagitta scrippsae*, described in Tables 1–28 are given in Figs. 2–4, and 6–30. Also included are illustrations of the four stages of maturity of *Eukrohnia bathyantarctica* (Fig. 1), *Krohnitta mutabbii* (Fig. 5), *Sagitta bierii* (Fig. 31), *S. elegans* (Fig. 32), *S. euneritica* (Fig. 33), *S. friderici* (Fig. 34), *S. gazellae* (Fig. 35), *S. helenae* (Fig. 36), *S. hispida* (Fig. 37), *S. marri* (Fig. 38), *S. maxima* (Fig. 39), *S. planctonis* (Fig. 40), *S. pseudoserratodentata* (Fig. 41), *S. serratodentata* (Fig. 42), *S. setosa* (Fig. 43), *S. tasmanica* (Fig. 44), and *S. tenuis* (Fig. 45).

Table 1
Maturity stages of *Eukrohnia bathypelagica* (Fig. 2)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear; vas deferens well developed	Ovaries small curled tubes	13 Fig. 2A
II	Tail filled with spermatids and sperm; seminal vesicles getting filled	Ovaries curled at top, reaching up to level of top of rayed zone in the paired fins	18 Fig. 2B
III	Tail full or partially empty; seminal vesicles full or broken	Ovaries curled at top, reaching up to 2/3 from ventral ganglion, in the distance to caudal septum	20 Fig. 2C
IV	Tail empty; seminal vesicles broken	Ovaries filling body cavity, reaching up to 1/3 from ventral ganglion, in the distance from there to caudal septum	23 Fig. 2D

Table 2
Maturity stages of *Eukrohnia fowleri* (Fig. 3)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as small rods with the upper part a little enlarged, extending along half the way in region of tail segment occupied by paired fins	Ovaries short and wide	12–21 Fig. 3A
II	Tail segment filled with spermatids; seminal vesicles beginning to appear	Ovaries reaching up to level of half of extent of rayed zone in the paired fins	25–32 Fig. 3B
III	Tail segment filled with spermatids and spermatozoids; seminal vesicles full	Ovaries with the ova large; seminal receptacle well apparent	34 Fig. 3C
IV	Tail segment partially discharged; seminal vesicles bursting	Ovaries with ova fully developed; seminal receptacle filled with sperm	> 35 Fig. 3D

Table 3
Maturity stages of *Eukrohnia hamata* (Fig. 4)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present	Ovaries as fine tubes	Up to 18 Fig. 4A
II	Tail segment filled with sperm; seminal vesicles incipient to full	Ovaries longer than in previous stage	23 Fig. 4B
III	Tail segment partially discharged; seminal vesicles broken	Ovaries increasing in length; ova developing	25 Fig. 4C
IV	Tail segment discharged; region of seminal vesicles covered by a thickening of epidermis	Ovaries reaching up to 2/3 of distance from ventral ganglion; ova fully developed	40 Fig. 4D

Table 4
Maturity stages of *Krohnitta pacifica* (Fig. 6)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes are fine tubes; caudal segment empty; no seminal vesicles visible	Ovaries reaching up to midlength of the extent of fins on trunk	4 Fig. 6A
II	Testes filling tail cavity; spermatids well visible; seminal vesicles beginning to appear	Ovaries reaching up to a level close to anterior end of the paired fins	5 Fig. 6B
III	Spermatozoids are well visible, filling tail cavity; seminal vesicles getting filled with sperm	Ovaries reaching up to midlength from ventral ganglion to anterior end of the paired fins	6–7 Fig. 6C
IV	Tail segment empty; seminal vesicles filled with sperm or broken	Ovaries reaching to region of ventral ganglion; filled with large ova arranged in one line	6–8 Fig. 6D

Table 5
Maturity stages of *Krohnitta subtilis* (Fig. 7)

Stage	Male gonads	Female gonads	Size (mm)
I	Tail segment getting filled with spermatids; seminal vesicles beginning to develop	Ovaries reaching up to 1/5 the length of the extent of the paired fins on trunk; ova small	Up to 10 Fig. 7A
II	Spermatozoids well visible in tail cavity; seminal vesicles beginning to get filled; cross-fertilization appears to take place during this stage; pouring of the sperm into seminal receptacle of another specimen's ovary	Ovaries reaching up to 1/2 the length of the extent of the paired fins on trunk	11–12 Fig. 7B
III	Tail segment empty; seminal vesicles appearing in a regenerative process	Ovaries reaching up to 2/3 the length of the extent of the paired fins on trunk	11–12 Fig. 7C
IV	Tail segment empty, and seminal vesicles appear either as in previous stage or tail filled with sperm and vesicles getting filled with male cells	Ovaries reaching up to anterior end of the paired fins	12–16 Fig. 7D

Table 6

Maturity stages of *Pterosagitta draco* (Fig. 8)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; tail segment empty; no seminal vesicles present	Ovaries as fine tubes reaching less than ¼ of length to neck	5–6 Fig. 8A
II	Tail segment filled with sperm; seminal vesicles filling or full	Ovaries reaching up to 2/3 of level from neck region	7 Fig. 8B
III	Tail segment empty; seminal vesicles empty	Ovaries reaching up to level of ventral ganglion	8 Fig. 8C
IV	Tail segment empty; seminal vesicles disappear	Ovaries filling body cavity, reaching up to neck region	9–10 Fig. 8D

Table 7

Maturity stages of *Sagitta bedfordii* (Fig. 9)

Stage	Male gonads	Female gonads	Size (mm)
III	Tail filled with sperm; seminal vesicles beginning to be filled	Ovaries reaching up to level of posterior end of anterior fins	2.8–3.0 Fig. 9C
IV	Tail totally or partially depleted of sperm; seminal vesicles bursting or full	Ovaries reaching up to level of region of ventral ganglion	3.5–4.0 Fig. 9D

Table 8

Maturity stages of *Sagitta bedoti* (Fig. 10)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present yet	Ovaries reaching up to near anterior end of posterior fins	9 Fig. 10A
II	Testes well visible, filling tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	11 Fig. 10B
III	Tail filled with spermatids and spermatozoids; seminal vesicles conspicuous, beginning to be filled with sperm	Ovaries reaching to level of posterior quarter of anterior fins	13–14 Fig. 10C
IV	Tail cavity beginning to empty sexual cells; seminal vesicles full or bursting	Ovaries reaching up to a level near region of ventral ganglion	14–15 Fig. 10D

Table 9

Maturity stages of *Sagitta bipunctata* (Fig. 11)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; seminal vesicles incipient	Ovaries are thin tubes, reaching up to the first quarter of the length of posterior fins along trunk	9 Fig. 11A
II	Testes filling the tail cavity; seminal vesicles well visible	Ovaries reach up to level of anterior end of posterior fins	11 Fig. 11B
III	Tail segment filled with spermatids; seminal vesicles are getting filled with sperm	Ovaries reach up to posterior end of posterior fins	13 Fig. 11C
IV	Tail segment filled or emptying the sexual products into the seminal vesicles which appear turgid and filled with sperm	Ovaries reach up to anterior third of anterior fins; ova round	14 Fig. 11D

Table 10

Maturity stages of *Sagitta bruuni* (Fig. 12)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as short, thin tubes; no seminal vesicles visible	Ovaries thin tubes, reaching up to level of midlength of the extent of posterior fins on trunk	8–10 Fig. 12A
II	Testes filling tail cavity; spermatids well visible; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	10–11 Fig. 12B
III	Tail cavity filled with spermatids and sperm; seminal vesicles beginning to be filled with sexual cells	Ovaries reaching up to posterior part of anterior fins	12 Fig. 12C
IV	Tail filled with sperm; seminal vesicles full	Ovaries reaching up to anterior quarter of anterior fins	14–15 Fig. 12D

Table 11

Maturity stages of *Sagitta decipiens* (Fig. 13)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear	Ovaries beginning to appear as small tubes	10 Fig. 13A
II	Testes filling tail cavity; seminal vesicles increasing in development	Ovaries reaching up to anterior end of posterior fins	12 Fig. 13B
III	Spermatids and spermatozoids filling tail cavity; seminal vesicles getting filled	Ovaries reaching up to posterior end of anterior fins	13–14 Fig. 13C
IV	Tail segment totally or partially empty; seminal vesicles full, bursting or discharged	Ovaries reaching level of anterior quarter of anterior fins	14–16 Fig. 13D

Table 12
Maturity stages of *Sagitta enflata* (Figs. 14 and 15)

Stage	Male gonads	Female gonads	Size[1]
I	No testes or vesicles visible	Ovaries reaching to 1/4 or 1/2 of length of posterior fins along trunk	Fig. 14A Fig. 15A
II	Testes well visible; seminal vesicles beginning to appear	Ovaries reaching to about midlength of the extent of posterior fins on trunk or near anterior end of posterior fins	Fig. 14B Fig. 15B
III	Testes filled with sperm; seminal vesicles beginning to be filled	Ovaries reaching to near anterior end of posterior fins or posterior end of anterior fins	Fig. 14C Fig. 15C
IV	Seminal vesicles full, bursting or already empty	Ovaries reaching to anterior end of posterior fins, or in the last cycle up to anterior fins; ova thus in small or in large number, respectively	Fig. 14D, G,H Fig. 15D

[1] Sizes are not given owing to the more or less continuous degree of variation.

Table 13
Maturity stages of *Sagitta ferox* (Fig. 16)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; no trace of seminal vesicles beginning to appear	Ovaries as fine tubes, reaching up to near anterior end of posterior fins	9 Fig. 16A
II	Tail filled with spermatids and sperm; seminal vesicles developing	Ovaries reaching up to midlength of anterior fins	12 Fig. 16B
III	Tail beginning to discharge sperm; seminal vesicles beginning to be filled	Ovaries reaching up to midway from neck to ventral ganglion	16 Fig. 16C
IV	Tail totally or partially empty; seminal vesicles full or discharged	Ovaries reaching up to neck region, filling body cavity; ova large, in two or three rows	17–18 Fig. 16D

Table 14
Maturity stages of *Sagitta hexaptera* (Fig. 17)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; seminal vesicles incipient	Ovaries like thin tubes, extending up to midlength of the extent of posterior fins on trunk	22 Fig. 17A
II	Testes filling the tail cavity; seminal vesicles developing	Ovaries reaching up to level of posterior end of anterior fins	27–30 Fig. 17B
III	Tail empty or partially emtpy; seminal vesicles full or broken	Ovaries reaching up close to level of posterior end of ventral ganglion	34 Fig. 17C
IV	Tail empty; seminal vesicles broken	Ovaries filled with large ova, reaching up to level of ventral ganglion	38–40 Fig. 17D

Table 15

Maturity stages of *Sagitta lyra* (Fig. 18)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles not present	Ovaries reaching up to ⅓ of the extent of posterior fins on trunk	17–22 Fig. 18A
II	Tail filled with spermatids; seminal vesicles beginning to appear	Ovaries reaching up to ¾ of length of posterior fins on trunk, or to anterior end of posterior fins	22–25 Fig. 18B
III	Tail segment filled with sperm, or emptying; seminal vesicles full	Ovaries reaching up to level of posterior third of anterior fins	27 Fig. 18C
IV	Tail segment empty; seminal vesicles empty	Ovaries reaching up to level of anterior end of anterior fins	30–38 Fig. 18D

Table 16

Maturity stages of *Sagitta macrocephala* (Fig. 19)

Stage	Male gonads	Female gonads	Size (mm)
I	No traces of testes or fine tubes apparent	No trace of ovaries, but when 14 mm long, ovaries reach up to 1/3 of extent of posterior fins on trunk	8–14 Fig. 19A
II	Testes as small rods at upper part of tail segment; seminal vesicles beginning to appear	Ovaries reaching up to level of midlength of extent of posterior fins on trunk	17 Fig. 19B
III	Testes filling tail cavity; seminal vesicles oval in shape, getting filled with sperm	Ovaries reaching up to a level close to posterior end of anterior fins	20–21 Fig. 19C
IV	Tail segment empty of sexual cells; seminal vesicles discharged	Ovaries reaching up to level of ventral ganglion; ova small and in four rows	22 Fig. 19D

Table 17

Maturity stages of *Sagitta minima* (Fig. 20)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes not yet visible or beginning to appear; seminal vesicles absent	Ovaries short, with small oocytes	4 Fig. 20A
II	Testes filling tail cavity; seminal vesicles beginning to develop	Ovaries reaching up to posterior third of length of posterior fins on trunk; oocytes of several orders visible	6–5 Fig. 20B
III	Spermatids and spermatozoids filling tail cavity; seminal vesicles beginning to be filled	Ovaries reaching up to midlength of extent of posterior fins on trunk; ova large	6–7 Fig. 20C
IV	Tail segment filled as in previous stage, partially or totally empty and seminal vesicles full	Ovaries reaching up to a level anterior to midlength of posterior fins on trunk; only three large ova per ovary found at this stage because one already released, as in the previous stage where four ova per ovary mostly seen	9–10 Fig. 20D

Table 18
Maturity stages of *Sagitta nagae* (Fig. 21)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; no seminal vesicles visible	Ovaries reaching up to level of half of anterior third of the extent of posterior fins on trunk	11–12 Fig. 21A
II	Testes filling tail cavity; seminal vesicles beginning to develop	Ovaries reaching up to posterior part of anterior fins	15 Fig. 21B
III	Tail cavity filled with spermatids and sperm; seminal vesicles beginning to be filled	Ovaries extending up to posterior fourth of anterior fins	19–20 Fig. 21C
IV	Tail cavity filled with sperm being released to seminal vesicles which are full	Ovaries reaching up to midlength of anterior fins	25 Fig. 21D

Table 19
Maturity stages of *Sagitta neglecta* (Fig. 22)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes appearing as thin tubes; seminal vesicles incipient	Ovaries as thin tubes reaching up to anterior third of extent of posterior fins on trunk	5 Fig. 22A
II	Testes filling tail cavity; spermatids well visible, seminal vesicles developing	Ovaries reaching up to level of midlength of anterior fins	6 Fig. 22B
III	Tail filled with sperm; seminal vesicles getting filled with spermatozoids	Ovaries reaching up to a level near anterior end of anterior fins	7 Fig. 22C
IV	Tail totally or partially empty; seminal vesicles full, bursting or broken	Ovaries reaching up to midway from neck to ventral ganglion, filling trunk cavity; ova large, round, and in one row	8 Fig. 22D

Table 20
Maturity stages of *Sagitta oceania* (Fig. 23)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as thin tubes or partially filling tail cavity	Ovaries reaching up to anterior end of posterior fins or to posterior end of anterior fins	4.4–8.0 Fig. 23A
II	Spermatids and sperm filling tail cavity; seminal vesicles beginning to be filled	Ovaries reaching to posterior part of anterior fins	4.9–5.0 Fig. 23B
III	Tail filled with sperm; seminal vesicles full	Ovaries reaching up to anterior end of anterior fins	5.0–5.5 Fig. 23C
IV	Tail partially or totally empty; seminal vesicles discharged	Ovaries reaching up to a level anterior to anterior end of ventral ganglion	5.5–6.5 Fig. 23D

Table 21
Maturity stages of *Sagitta pacifica* (Fig. 24)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles beginning to appear	Ovaries as fine tubes, reaching up to level of anterior end of posterior fins	7 Fig. 24A
II	Testes filling tail cavity; seminal vesicles conspicuous	Ovaries reaching up to posterior end of anterior fins	9–10 Fig. 24B
III	Tail filled with spermatogonia and spermatozoids; seminal vesicles turgid, filled with sperm	Ovaries reaching up to anterior quarter of anterior fins	10–11 Fig. 24C
IV	Tail partially or totally empty; seminal vesicles full or empty	Ovaries with large ova, filling body cavity and reaching up to level of ventral ganglion or close to neck	12–14 Fig. 24D

Table 22
Maturity stages of *Sagitta pulchra* (Fig. 25)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes visible; seminal vesicles beginning to appear	Ovaries like thin tubes reaching up to a level close to anterior end of posterior fins	18 Fig. 25A
II	Tail filled with spermatogonia; seminal vesicles developing	Ovaries reaching up to posterior end of anterior fins	20–22 Fig. 25B
III	Tail filled with sperm; seminal vesicles beginning to get filled	Ovaries reaching up to level of midlength of anterior fins	23 Fig. 25C
IV	Tail empty; seminal vesicles full	Ovaries reaching up to level of ventral ganglion	23–24 Fig. 25D

Table 23
Maturity stages of *Sagitta regularis* (Fig. 26)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear as small thread-like tubes; no seminal vesicles visible	Ovaries as thin tubes, reaching up to anterior end of posterior fins	3.0–3.7 Fig. 26A
II	Testes filling tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to posterior part of anterior fins	4 Fig. 26B
III	The tail cavity completely filled with spermatids and spermatozoids; seminal vesicles getting filled with sperm	Ovaries reaching up to midlength of anterior fins	5 Fig. 26C
IV	Tail segment almost empty; seminal vesicles swollen and filled with sperm	Ovaries reaching further or up to level of ventral ganglion; ova large, oval and elongated along the longitudinal axis and distributed in one row	6 Fig. 26D

Table 24

Maturity stages of *Sagitta robusta* (Fig. 27)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles incipient	Ovaries reaching up to level of anterior end of posterior fins	6–8 Fig. 27A
II	Testes filling tail cavity; spermatids well visible and spermatozoids beginning to appear; seminal vesicles conspicuous	Ovaries reaching up to anterior part of anterior end of anterior fins	10 Fig. 27B
III	Tail filled with sperm; seminal vesicles filled with sperm	Ovaries reaching up to midway of distance from neck to ventral ganglion	11–12 Fig. 27C
IV	Tail partially or totally empty; seminal vesicles filled with sperm	Ovaries reaching up to anterior septum at neck, filling trunk cavity	12 Fig. 27D

Table 25

Maturity stages of *Sagitta scrippsae*

Stage	Male gonads	Female gonads	Size (mm)
I	Testes present	Ovaries beginning to appear	7–30
II	Tail segment filled with sperm; seminal vesicles beginning to appear	Ovaries reach up to the anterior end of posterior fins in the most advanced phase of this stage	31–38
III	Transfer of sperm from the tail segment to the seminal vesicles	Ovaries reach to the middle of anterior fins	39–49
IV	Tail empty; seminal vesicles ready to burst, or broken and discharged	Ovaries reach near the neck region; seminal receptacles filled with spermatozoa; ova polygonal in shape, distributed in five or six stacked rows	50–60

Table 26

Maturity stages of *Sagitta septata* (Fig. 28)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes; seminal vesicles incipient	Ovaries reaching up to level of anterior end of posterior fins	4.5–5.0 Fig. 28A
II	Testes filling tail cavity; spermatids and sperm visible; seminal vesicles developing	Ovaries reaching up to level of posterior end of anterior fins	5.5 Fig. 28B
III	Tail cavity partially emptied of sperm; seminal vesicles full or bursting	Ovaries reaching up to level of ventral ganglion	5.5–6.0 Fig. 28C
IV	Tail cavity empty; seminal vesicles empty	Ovaries reaching up to neck; ova in one line with 20–30 ova per ovary	6 Fig. 28D

Table 27
Maturity stages of *Sagitta tokiokai* (Fig. 29)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes as fine tubes, or beginning to fill tail cavity; seminal vesicles beginning to appear	Ovaries reaching up to level of anterior end of posterior fins	13 Fig. 29A
II	Testes filling tail cavity; spermatids and bunches of sperm can be seen; seminal vesicles developing	Ovaries extending up to posterior third of anterior fins	15 Fig. 29B
III	Tail cavity filled with sperm; seminal vesicles filled with sexual cells	Ovaries reaching close to level of ventral ganglion	18 Fig. 29C
IV	Sperm still in tail cavity; seminal vesicles full	Ovaries reaching up to anterior septum, filling trunk cavity; ova in three or four rows	19–22 Fig. 29D

Table 28
Maturity stages of *Sagitta zetesios* (Fig. 30)

Stage	Male gonads	Female gonads	Size (mm)
I	Testes beginning to appear; no seminal vesicles apparent	Ovaries beginning to appear as thin tubes, extending to about half the extent of posterior fins on trunk	20 Fig. 30A
II	Testes filling the tail cavity; spermatogonia clearly visible; seminal vesicles beginning to appear	Ovaries as fine tubes reaching up to a level anterior to anterior end of anterior fins	29 Fig. 30B
III	Tail filled with spermatogonia and sperm; seminal vesicles oval, beginning to be filled	Ovaries as thin tubes reaching up to level of middle of anterior third of anterior fins	32–34 Fig. 30C
IV	Seminal vesicles filled or broken; an oval groove indicating place once occupied by vesicles	Ovaries reaching up to midway between neck and ventral ganglion	39–43 Fig. 30D

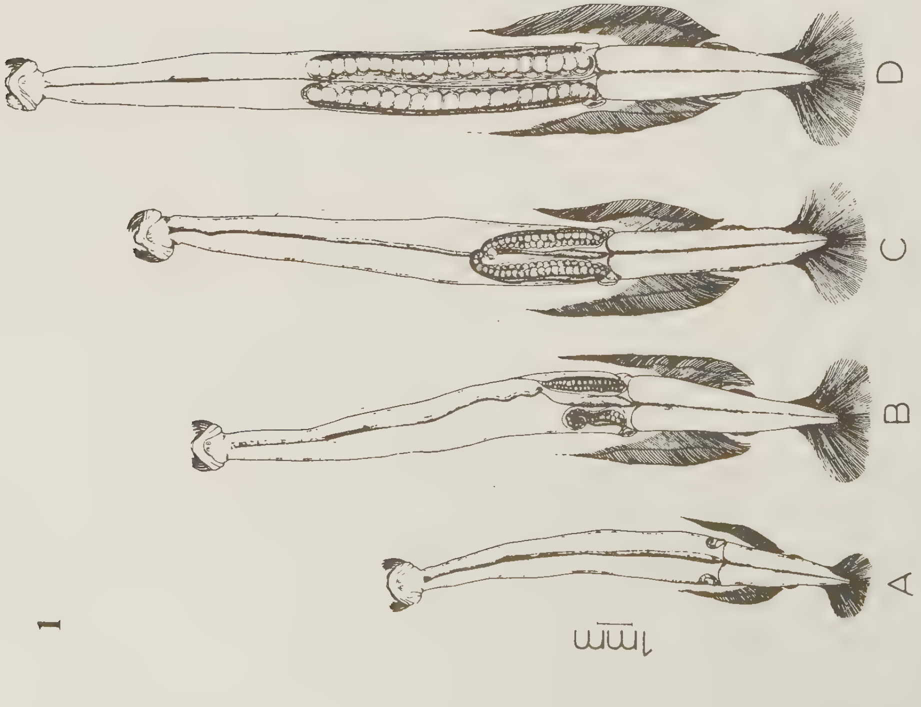

Fig. 1. Four stages of maturity of *Eukrohnia bathyantarctica.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

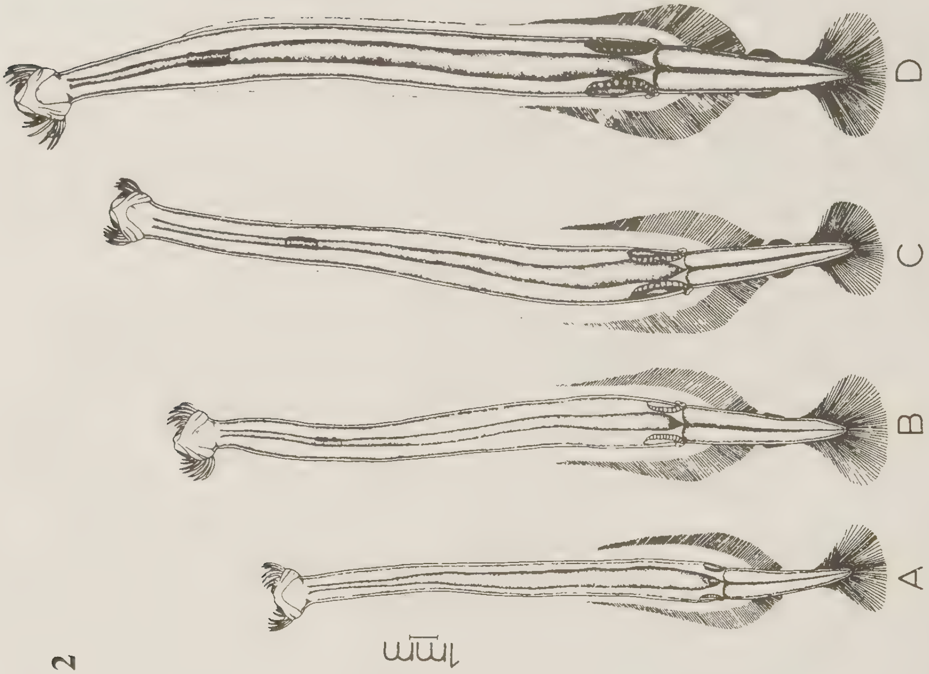

Fig. 2. Four stages of maturity of *Eukrohnia bathypelagica.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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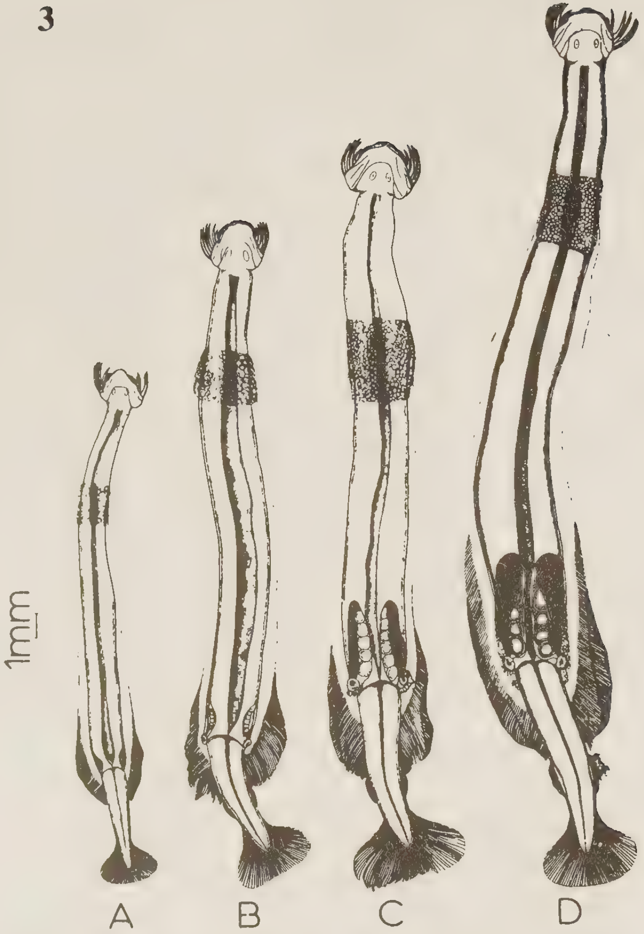

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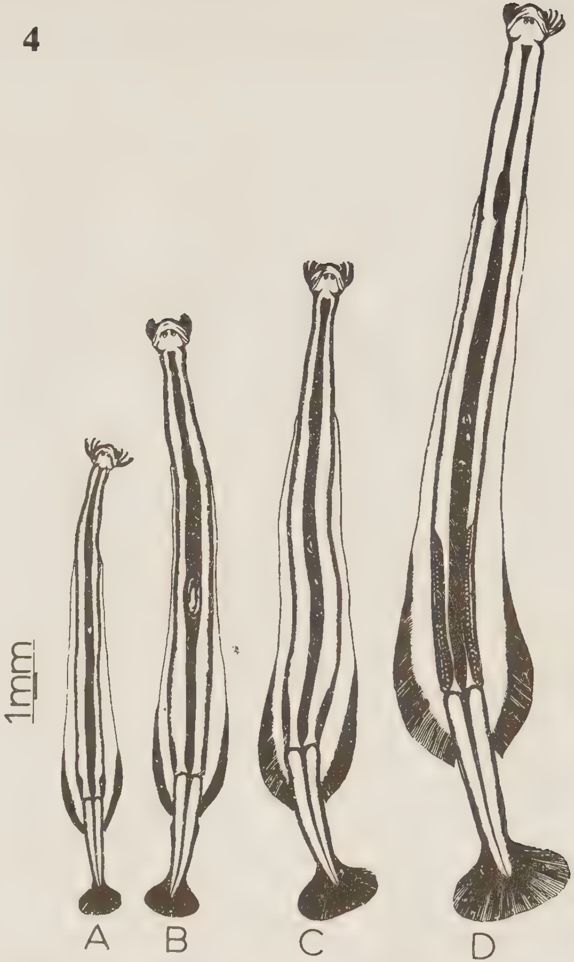

Fig. 3. Four stages of maturity of *Eukrohnia fowleri.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 4. Four stages of maturity of *Eukrohnia hamata.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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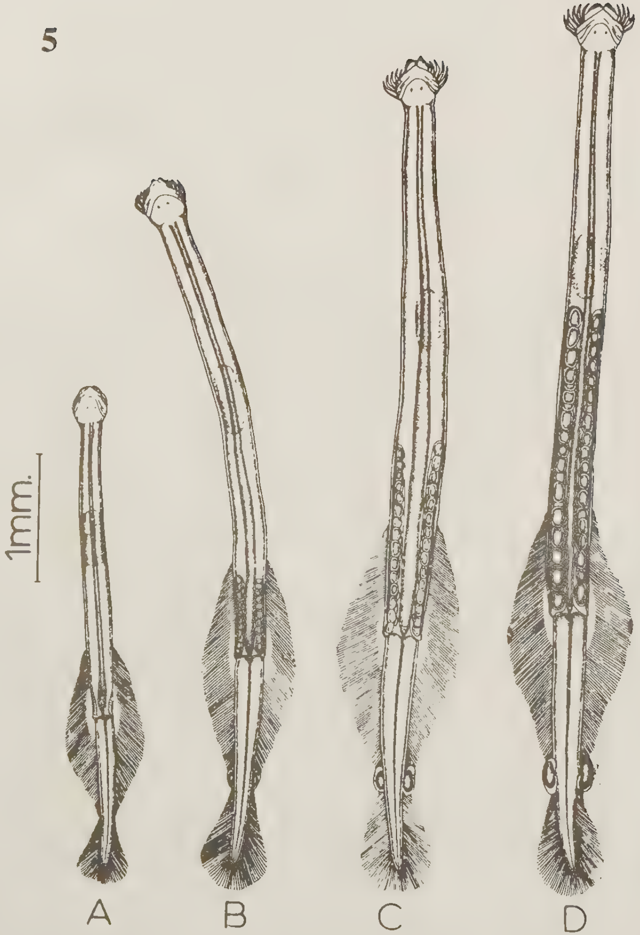

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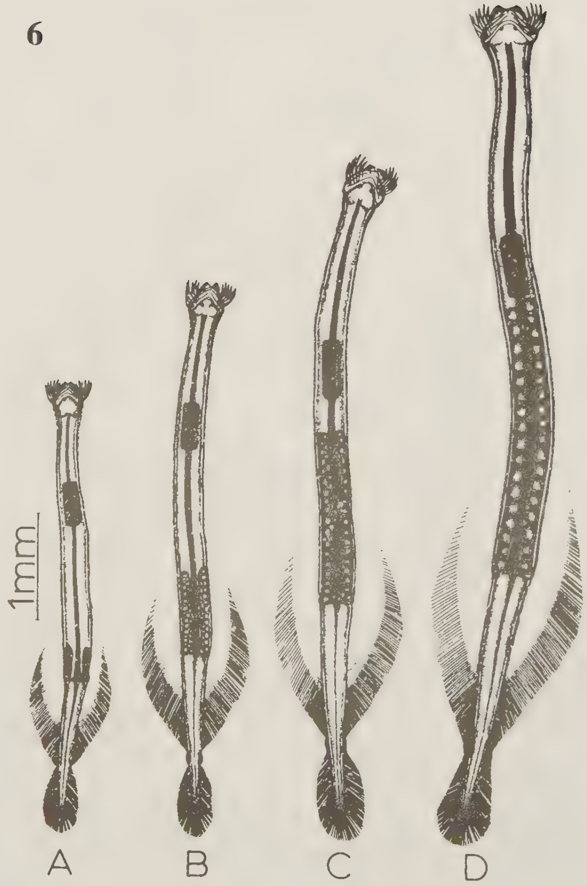

Fig. 5. Four stages of maturity of *Krohnitta mutabbii*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 6. Four stages of maturity of *Krohnitta pacifica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

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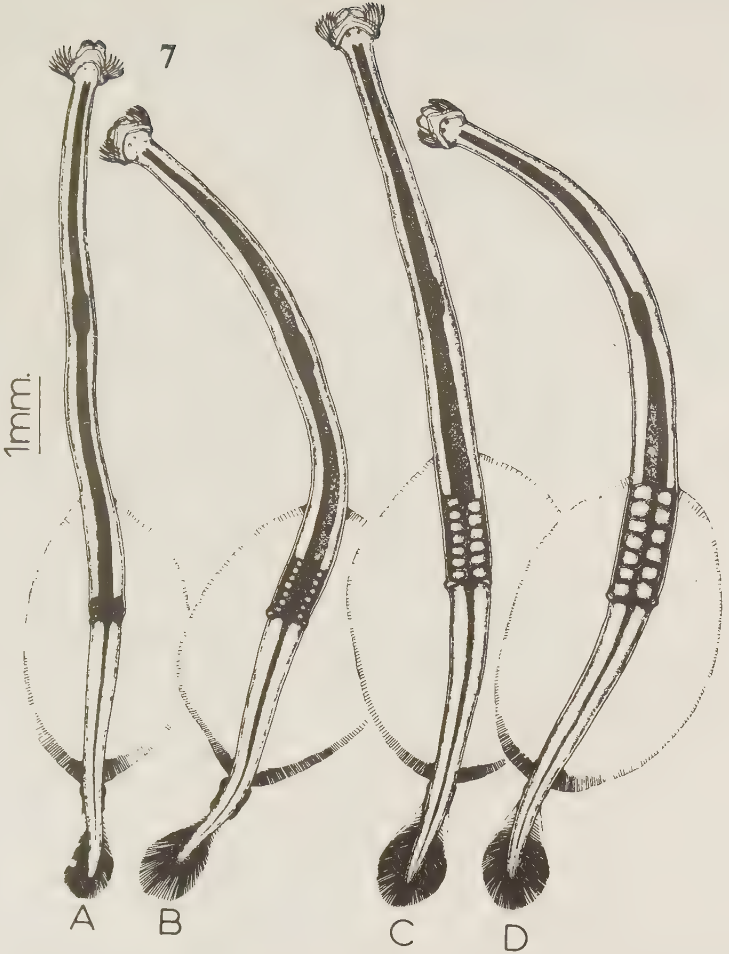

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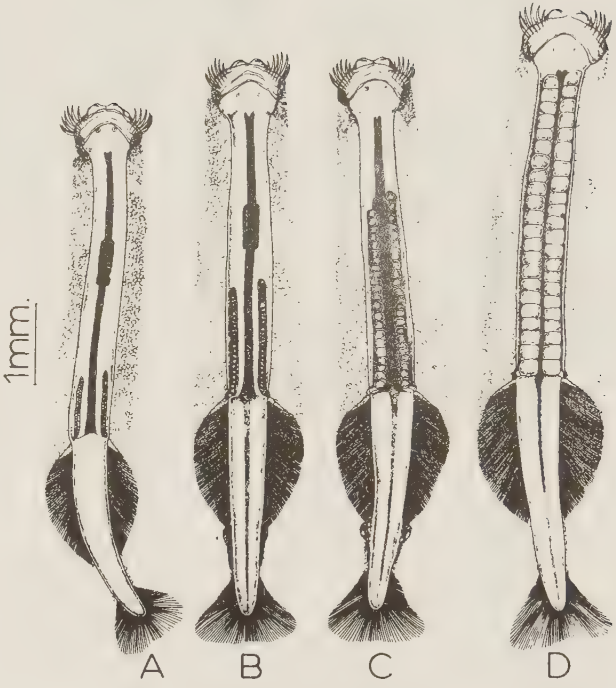

Fig. 7. Four stages of maturity of *Krohnitta subtilis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 8. Four stages of maturity of *Pterosagitta draco*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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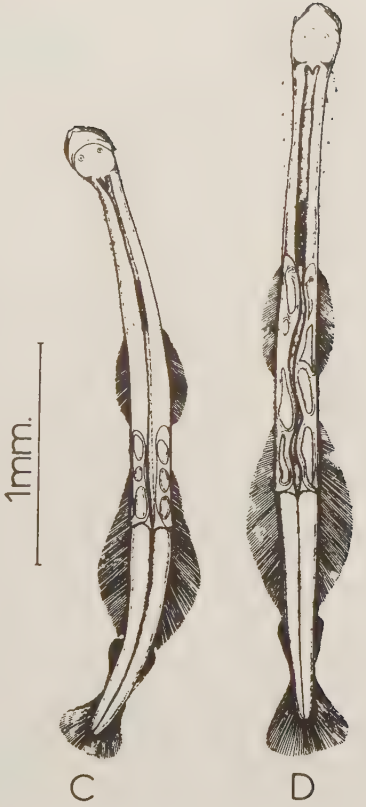

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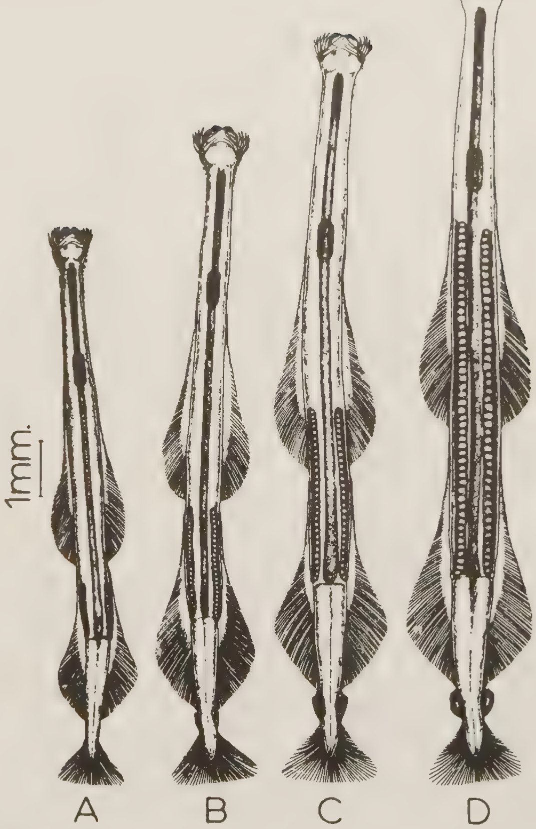

Fig. 9. Two stages in development of *Sagitta bedfordii.* **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 10. Four stages of maturity of *Sagitta bedoti.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

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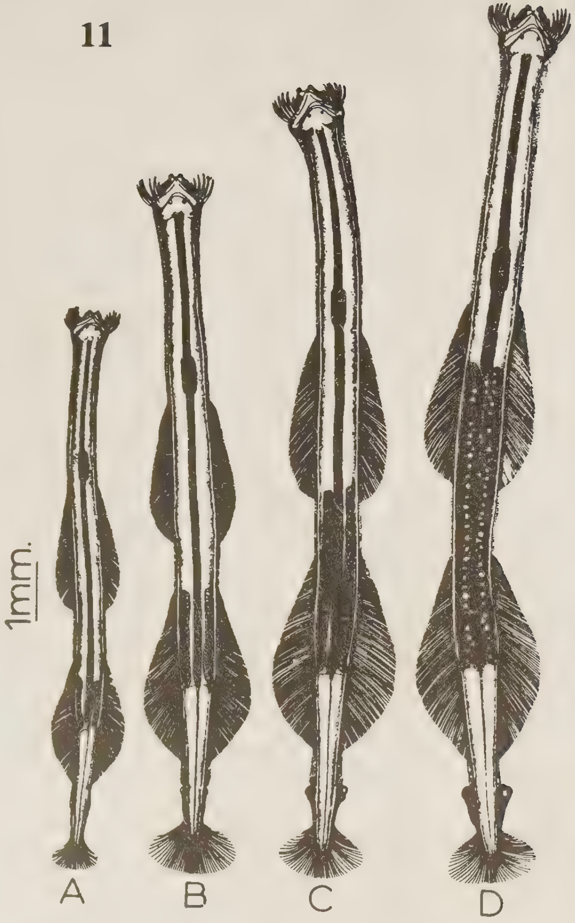

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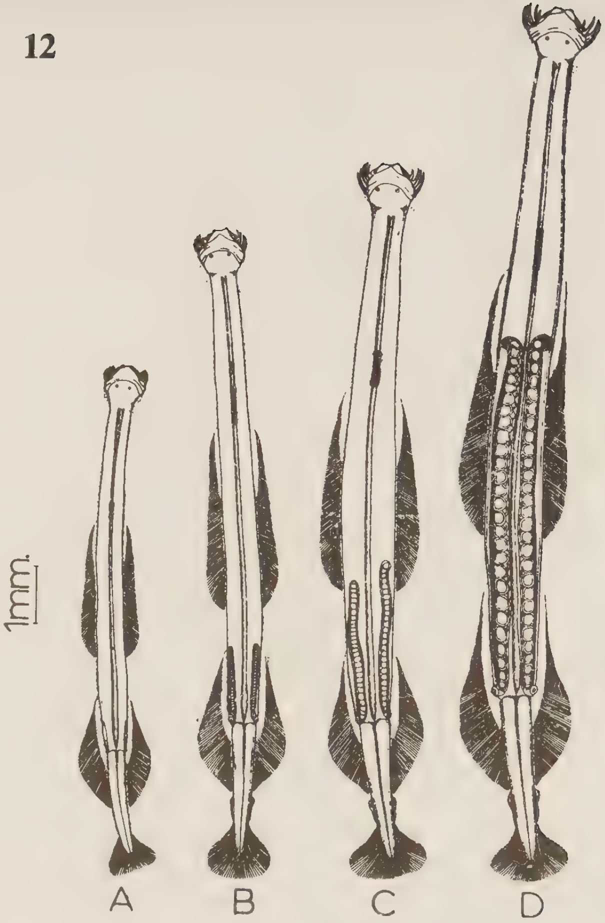

Fig. 11. Four stages of maturity of *Sagitta bipunctata*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 12. Four stages of maturity of *Sagitta bruuni*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

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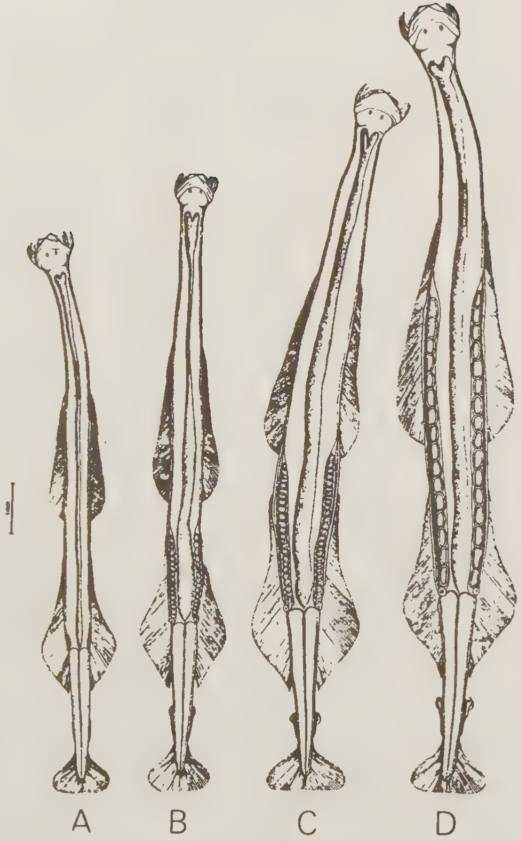

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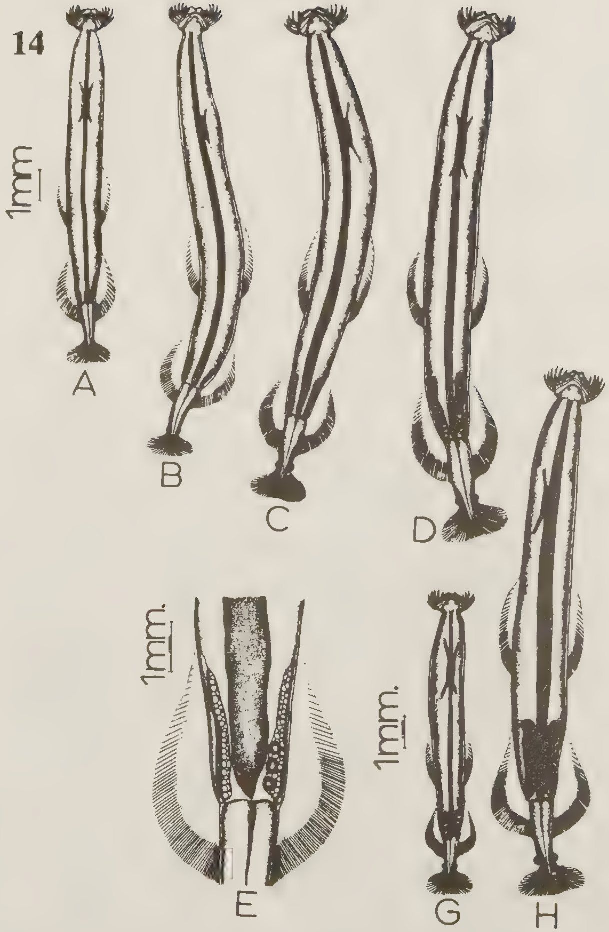

Fig. 13. Four stages of maturity of *Sagitta decipiens.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 14. Four stages of maturity of *Sagitta enflata.* **A:** Stage I second cycle; **B:** Stage II second cycle; **C:** Stage III second cycle; **D and H:** Stage IV second cycle; **E:** Detail of ovaries in the developing period of second cycle, **G:** Stage IV first maturity cycle. (From Alvariño, 1963, 1967, 1969.)

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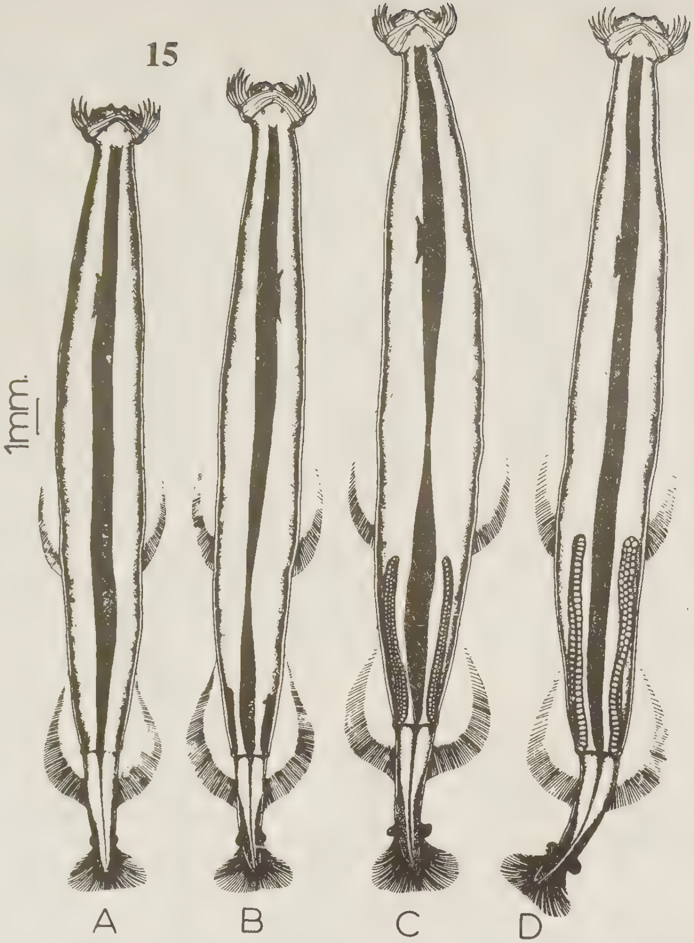

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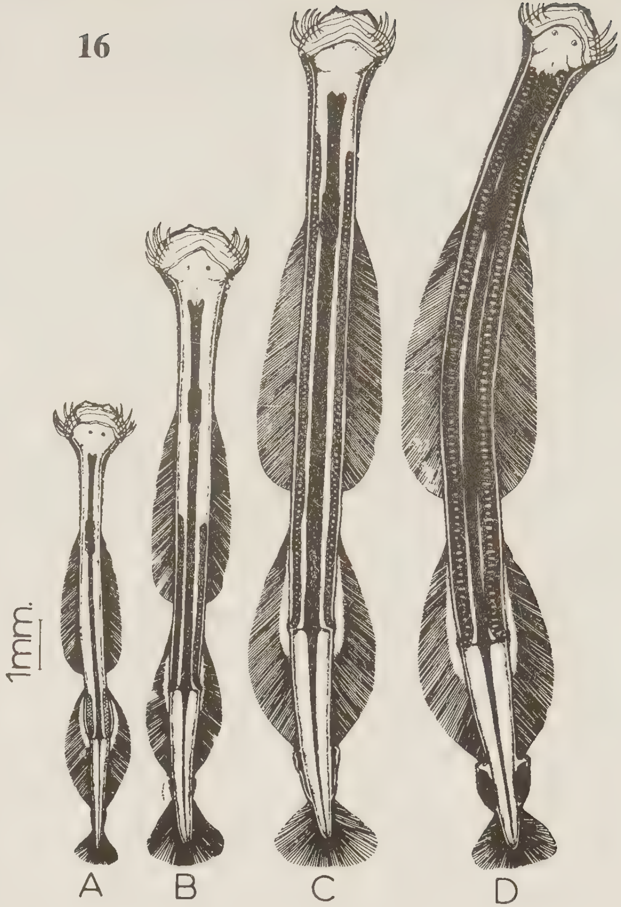

Fig. 15. Four stages of maturity of *S. enflata*, last cycle. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 16. Four stages of maturity of *Sagitta ferox*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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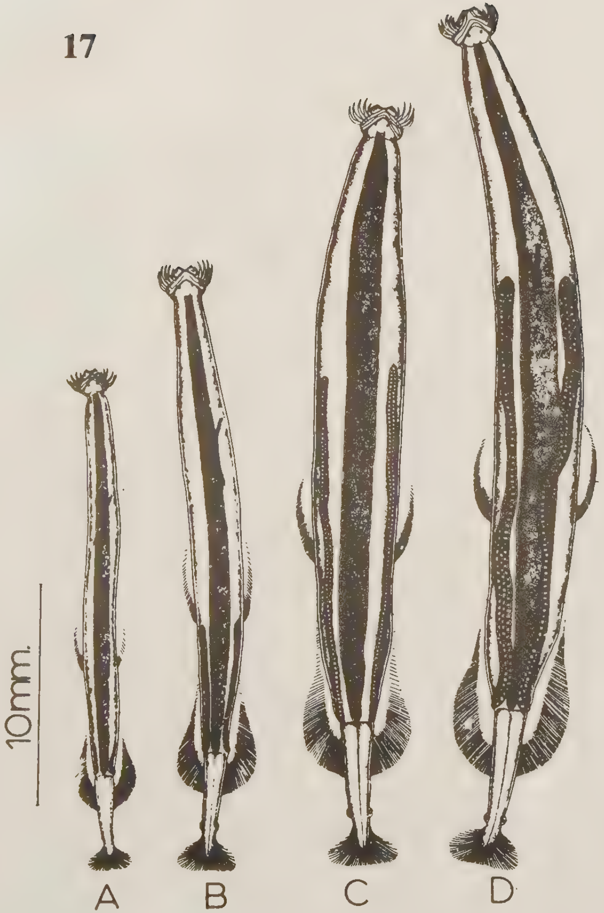

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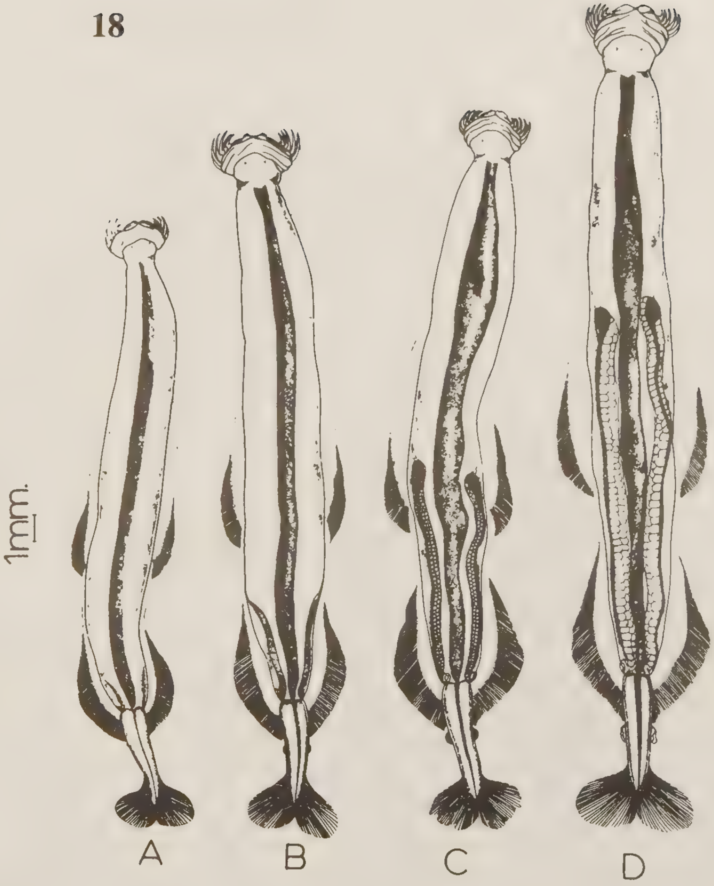

Fig. 17. Four stages of maturity of *Sagitta hexaptera.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

Fig. 18. Four stages of maturity of *Sagitta lyra.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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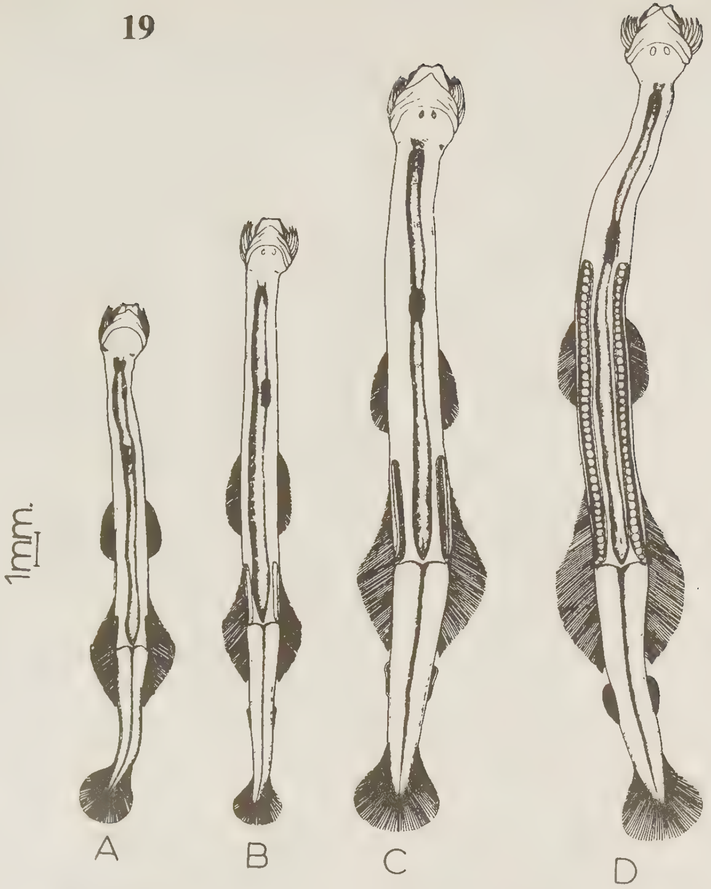

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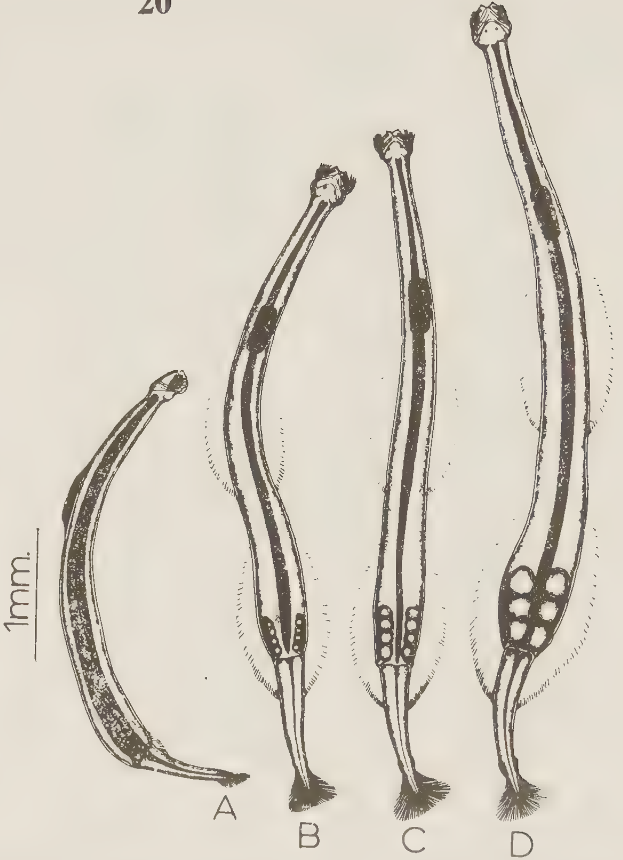

Fig. 19. Four stages of maturity of *Sagitta macrocephala*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

Fig. 20. Four stages of maturity of *Sagitta minima*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967, 1969.)

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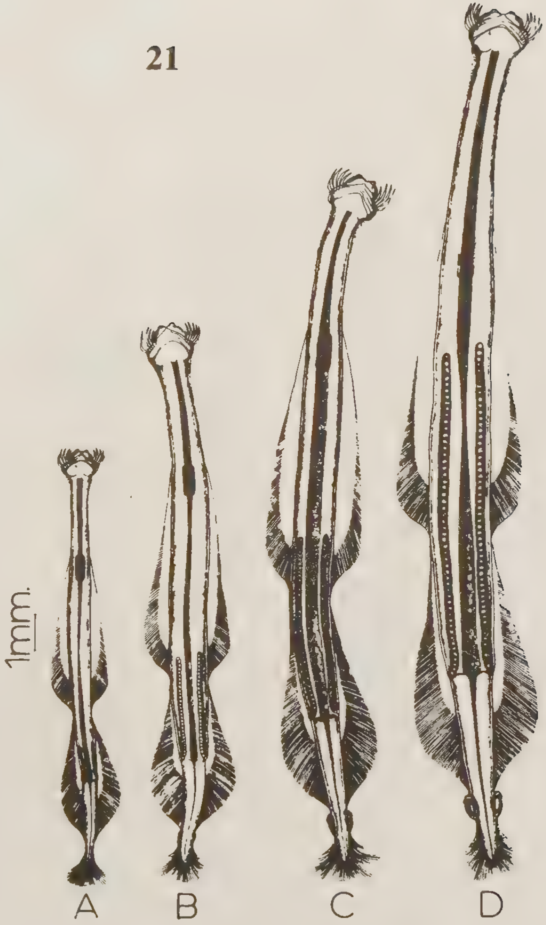

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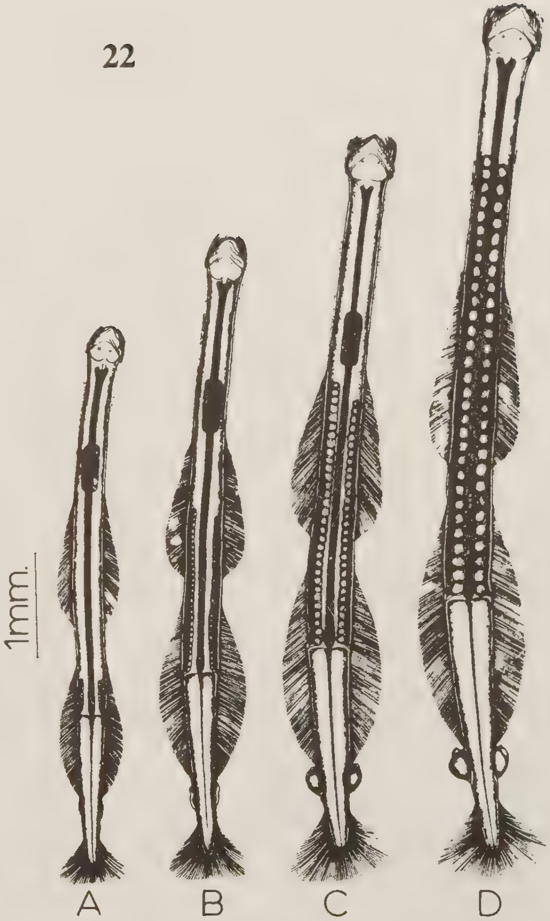

Fig. 21. Four stages of maturity of *Sagitta nagae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 22. Four stages of maturity of *Sagitta neglecta*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

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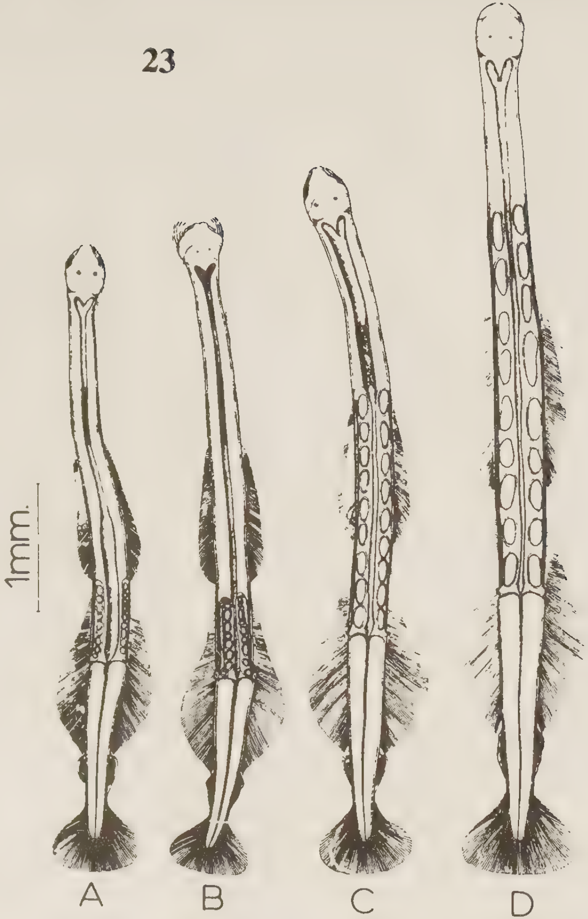

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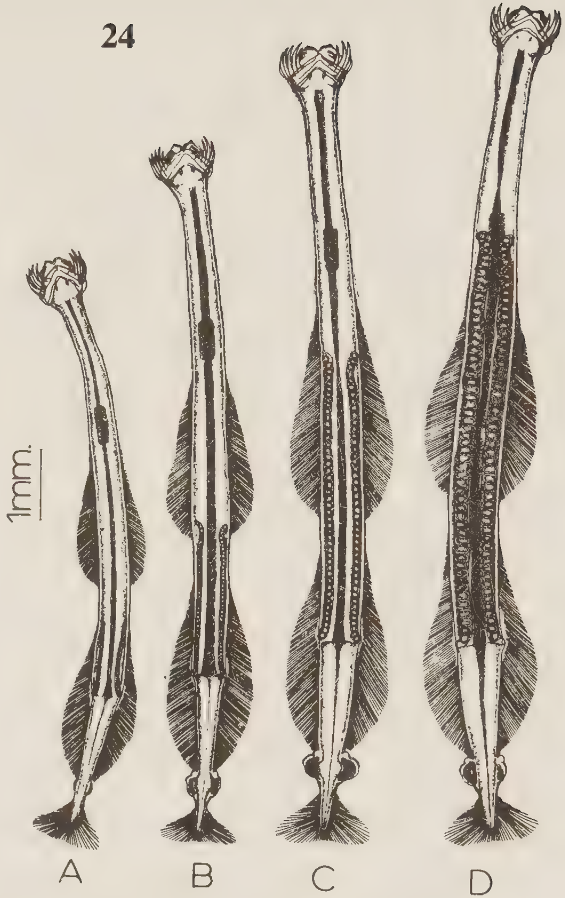

Fig. 23. Four stages of maturity of *Sagitta oceania*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967)

Fig. 24. Four stages of maturity of *Sagitta pacifica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

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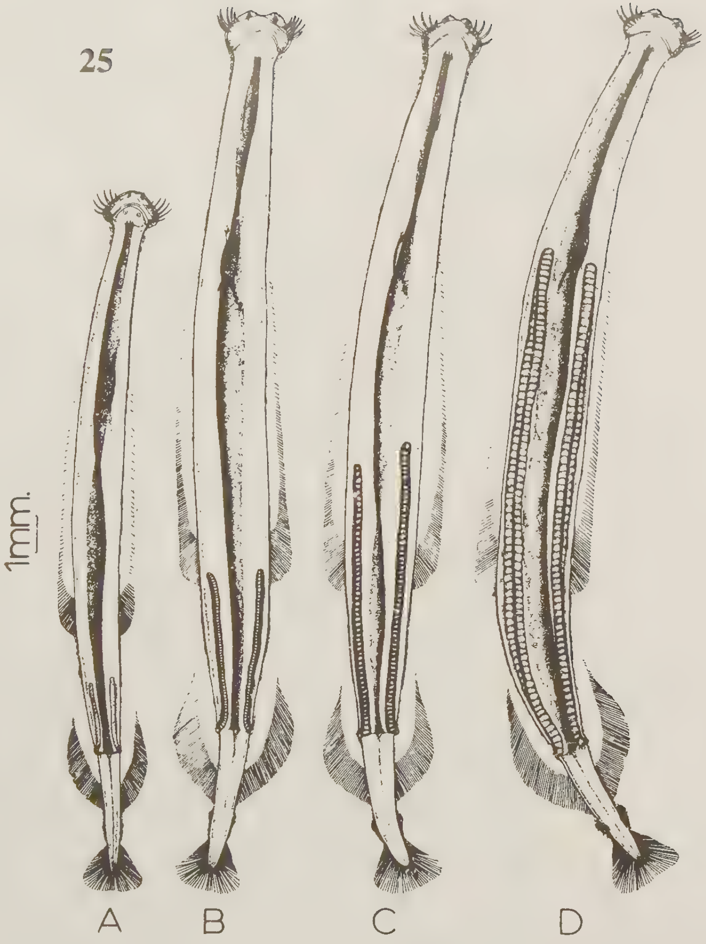

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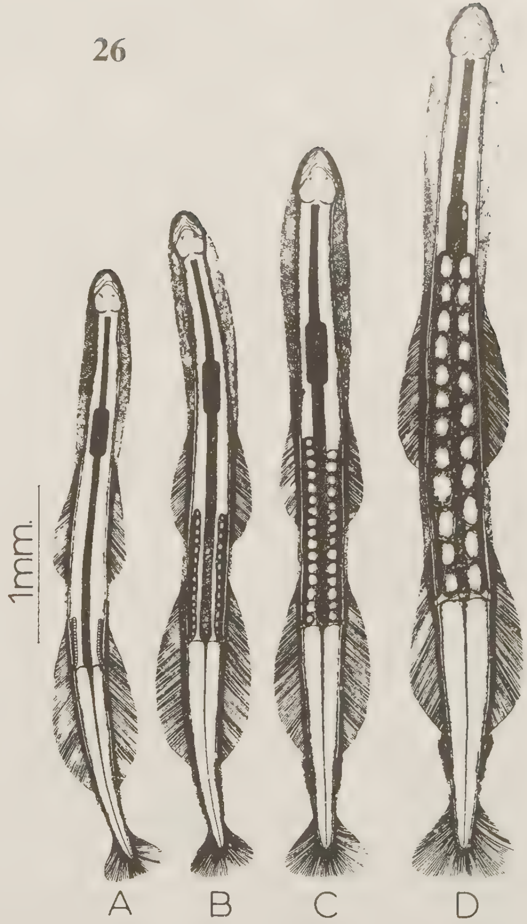

Fig. 25. Four stages of maturity of *Sagitta pulchra.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 26. Four stages of maturity of *Sagitta regularis.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963, 1967.)

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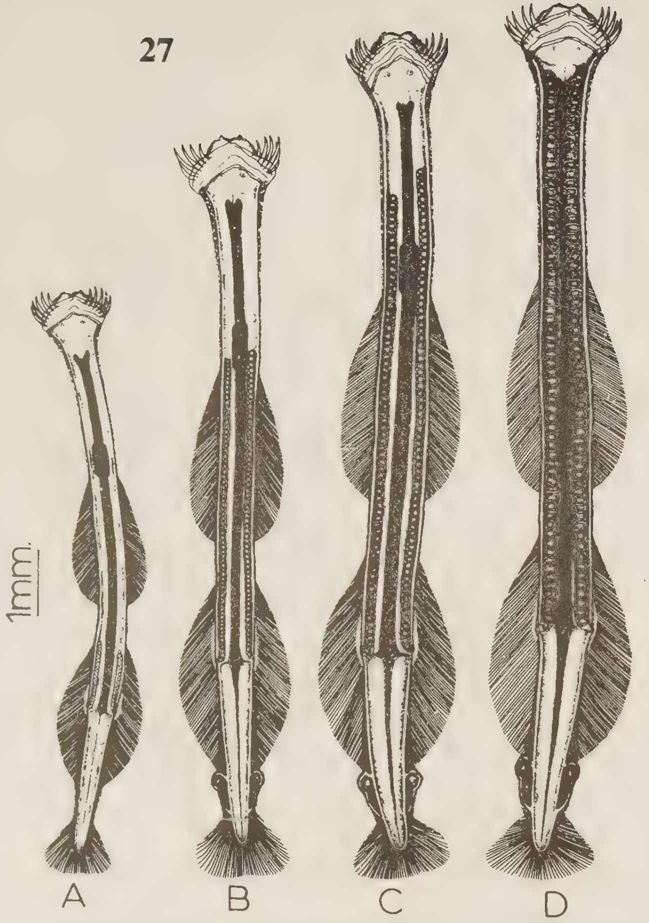

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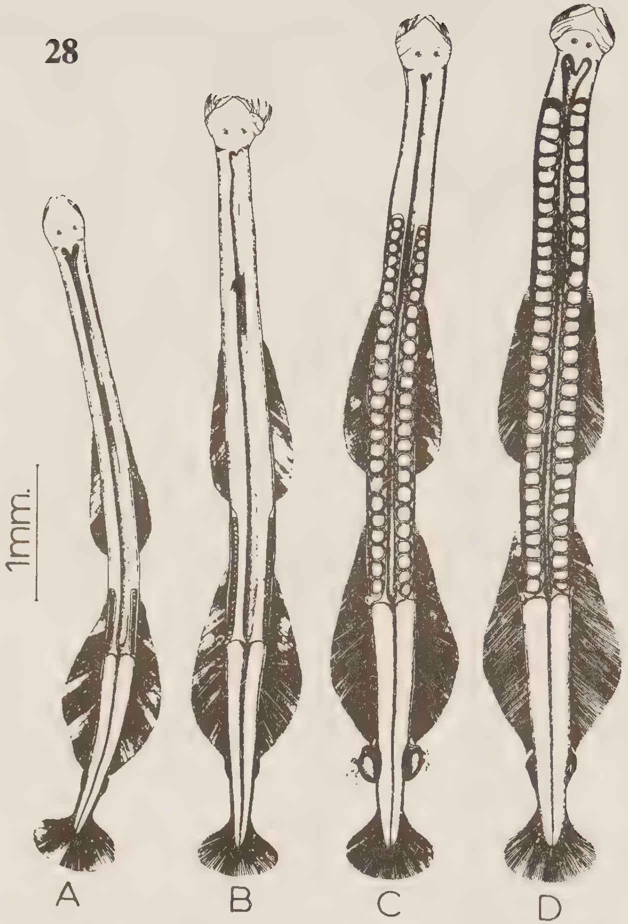

Fig. 27. Four stages of maturity of *Sagitta robusta.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 28. Four stages of maturity of *Sagitta septata.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

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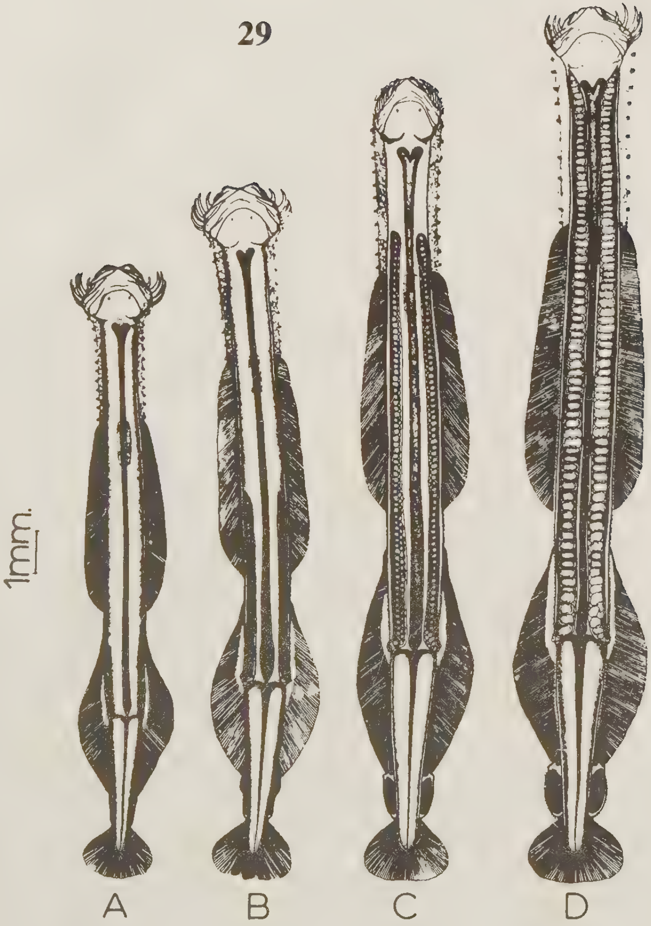

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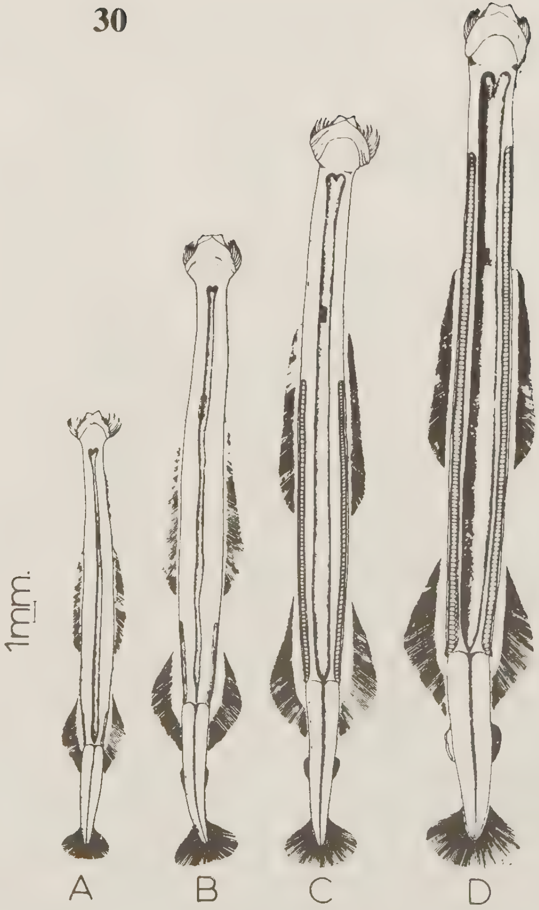

Fig. 29. Four stages of maturity of *Sagitta tokiokai.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967.)

Fig. 30. Four stages of maturity of *Sagitta zetesios.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1967, 1969.)

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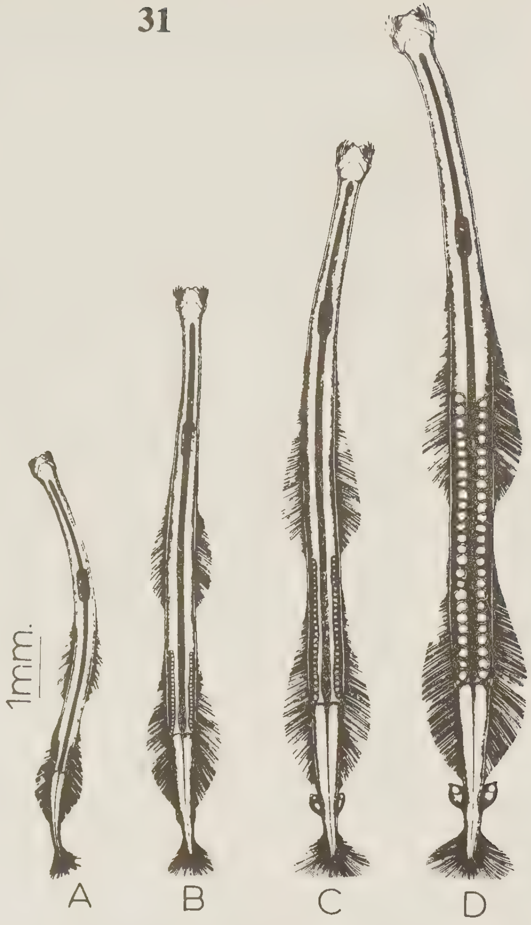

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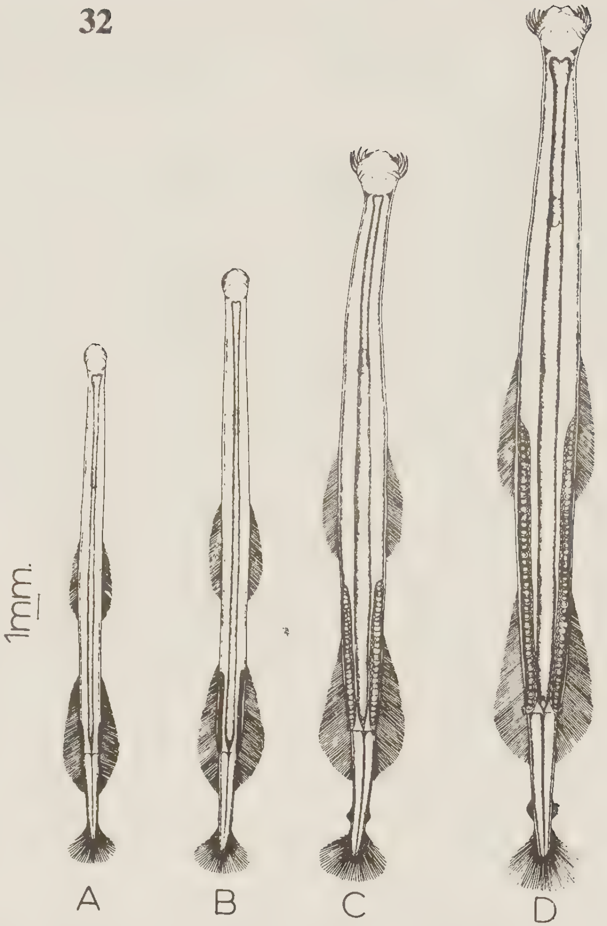

Fig. 31. Four stages of maturity of *Sagitta bierii.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963.)

Fig. 32. Four stages of maturity of *Sagitta elegans.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

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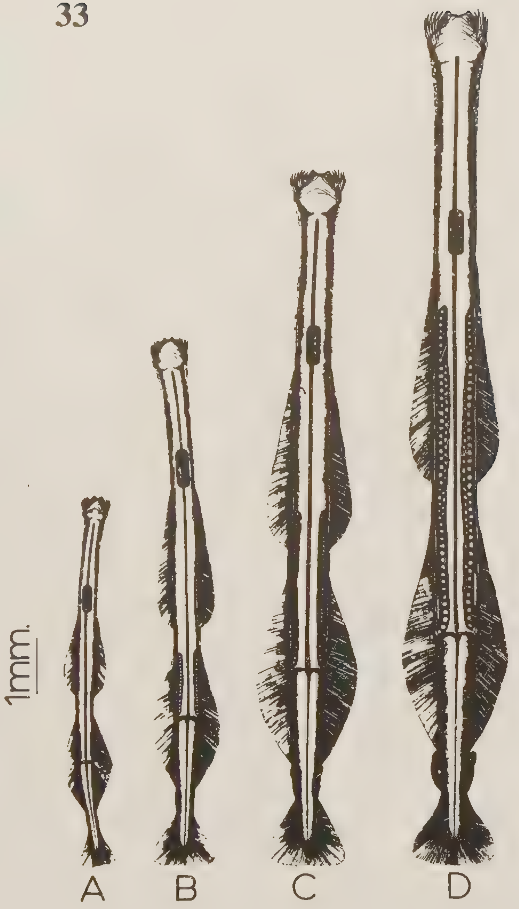

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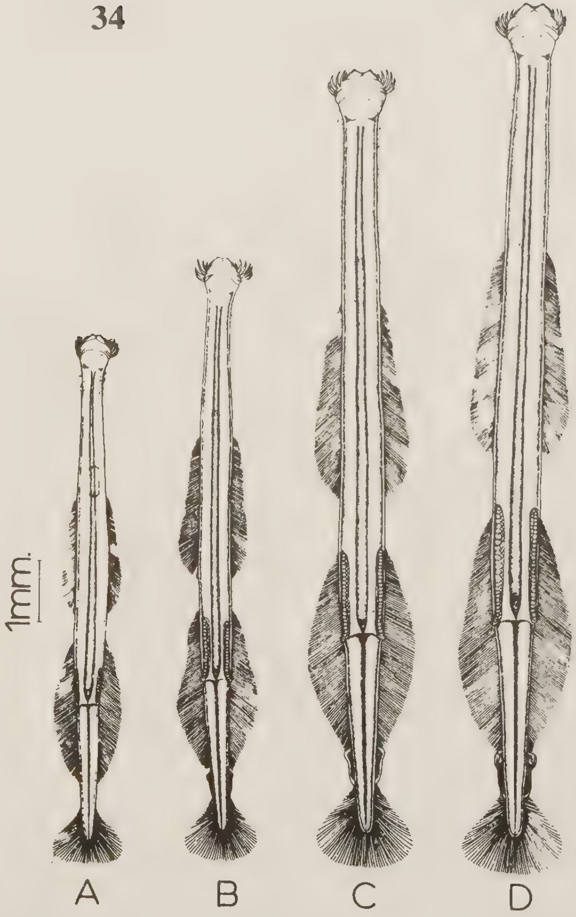

Fig. 33. Four stages of maturity of *Sagitta euneritica.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963.)

Fig. 34. Four stages of maturity of *Sagitta friderici.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

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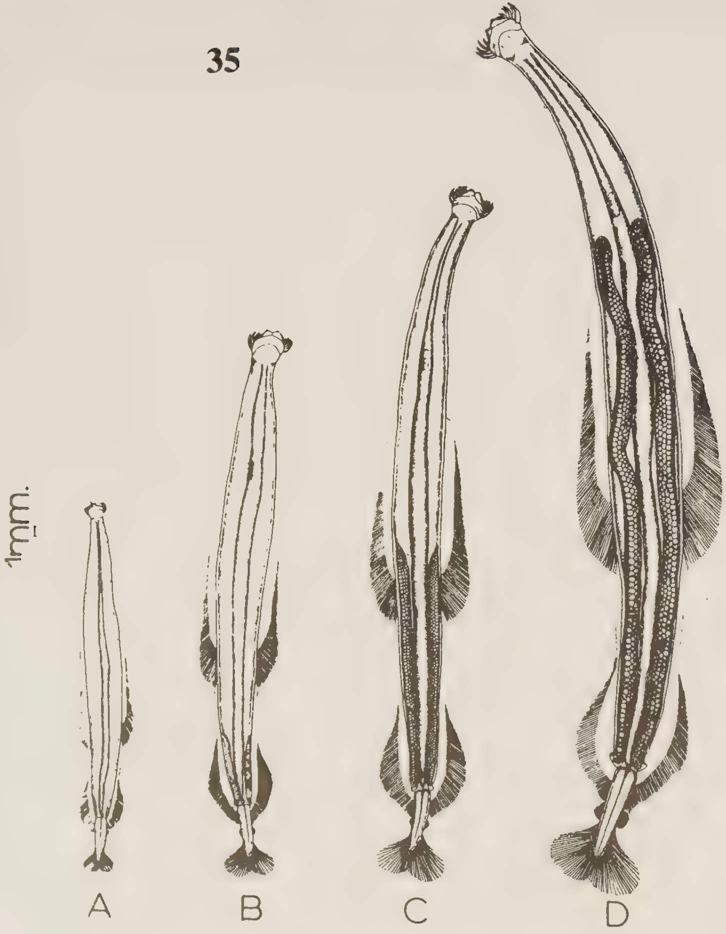

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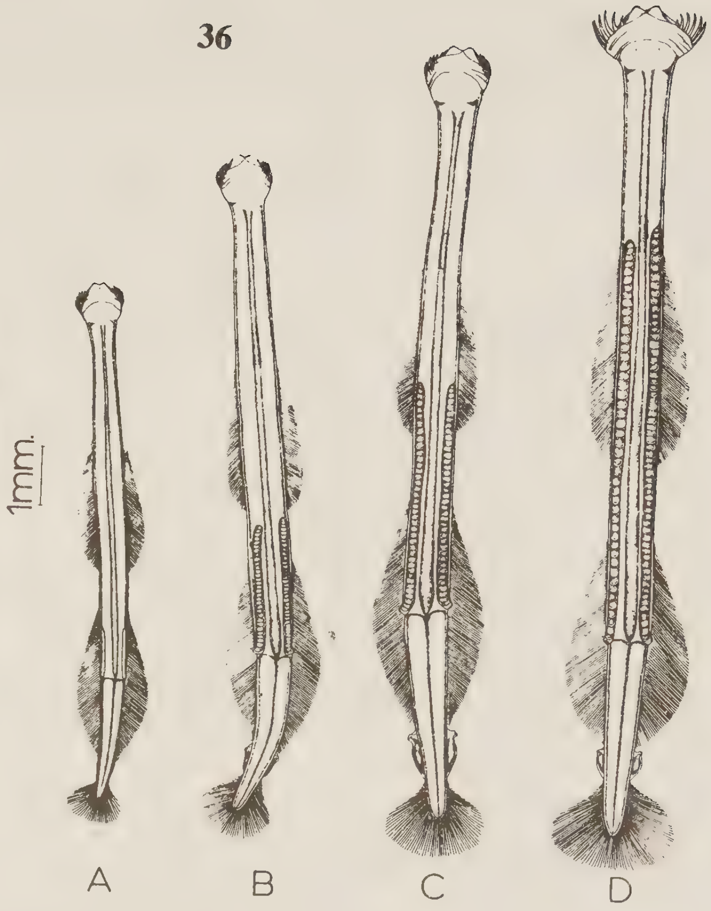
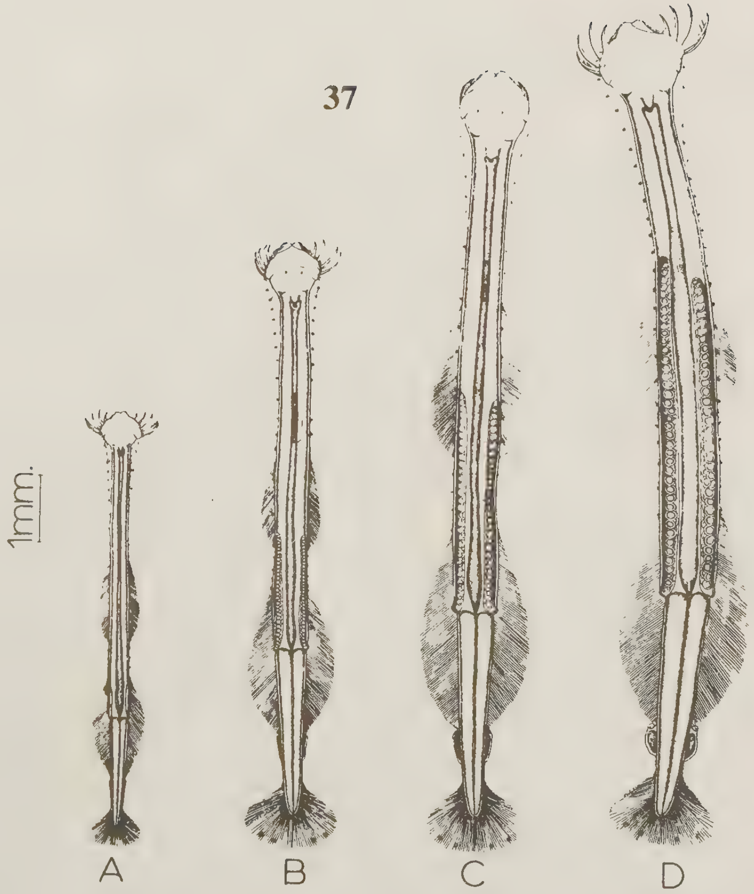


Fig. 35. Four stages of maturity of *Sagitta gazellae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 36. Four stages of maturity of *Sagitta helenae*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

37



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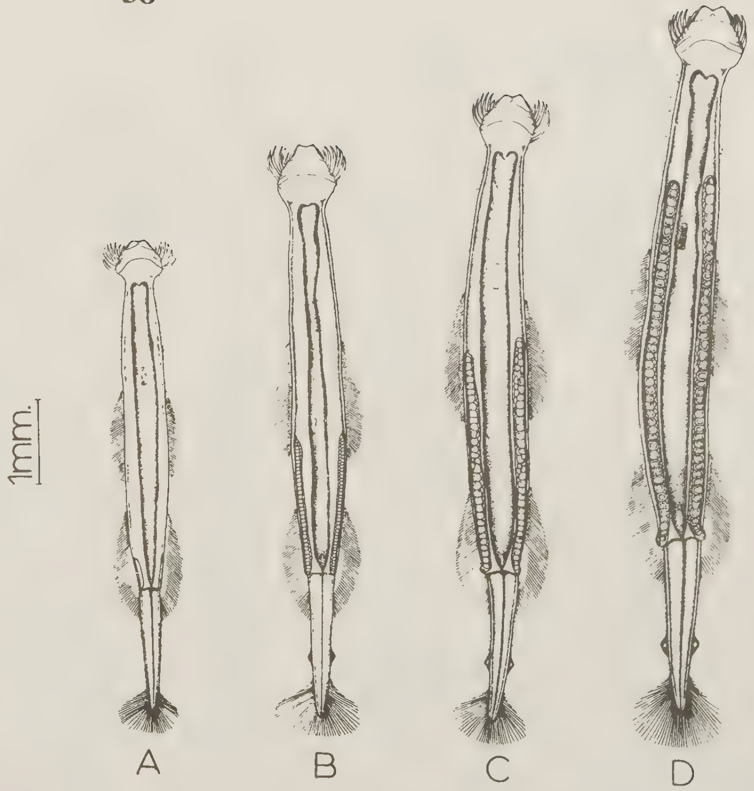
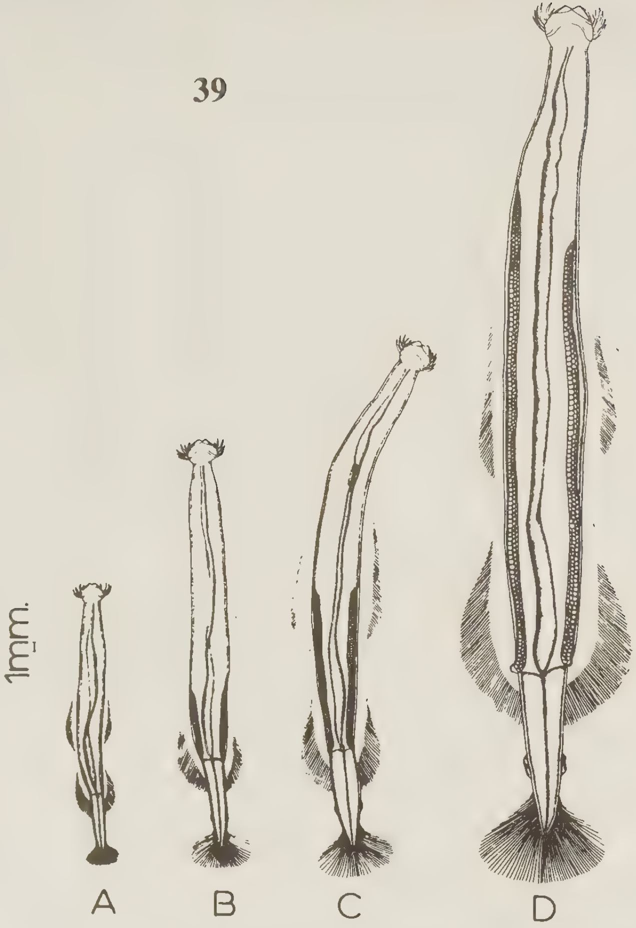


Fig. 37. Four stages of maturity of *Sagitta hispida.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 38. Four stages of maturity of *Sagitta marri.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

39



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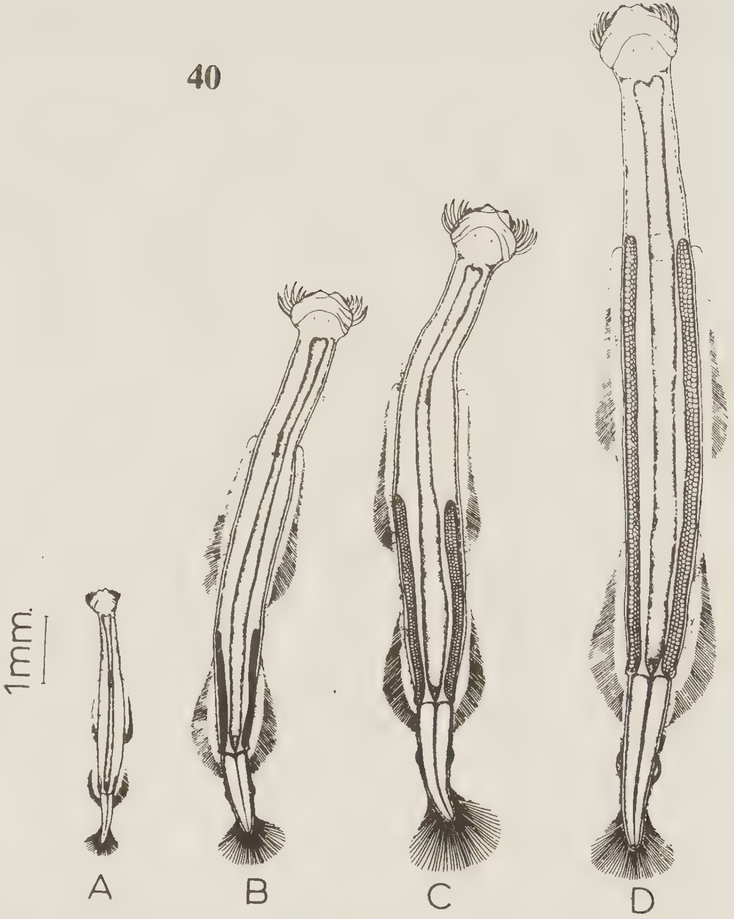
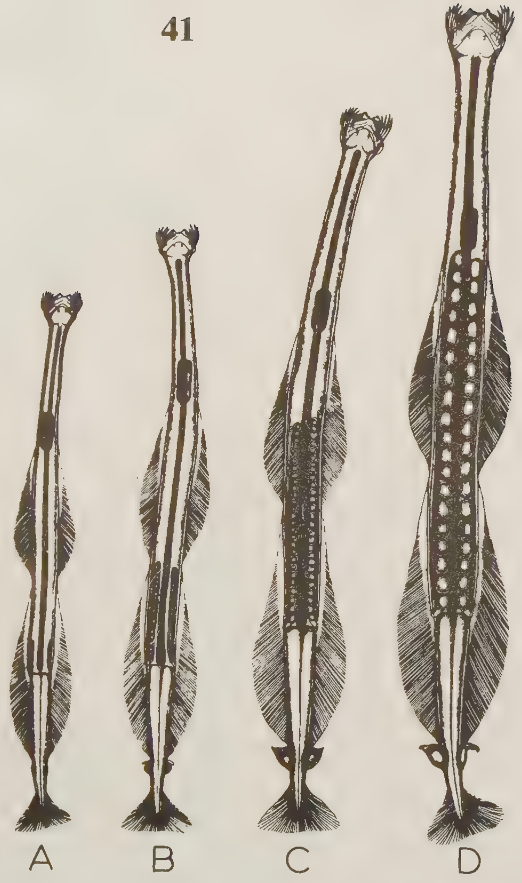


Fig. 39. Four stages of maturity of *Sagitta maxima*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 40. Four stages of maturity of *Sagitta planctonis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

41



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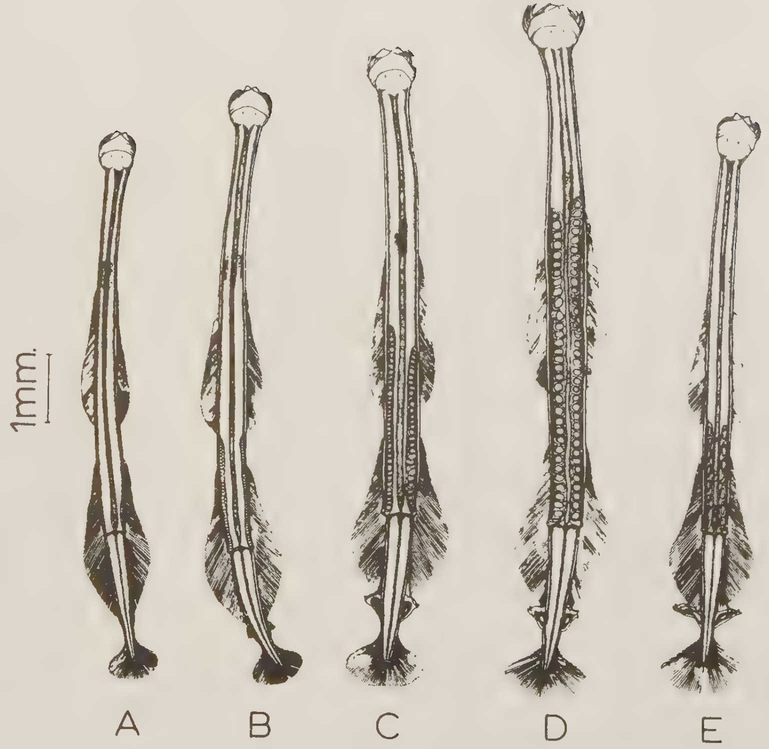

Fig. 41. Four stages of maturity of *Sagitta pseudoserratodentata.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1963.)

Fig. 42. Stages of maturity of *Sagitta serratodentata.* **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV; **E:** spent. (From Alvariño, 1969.)

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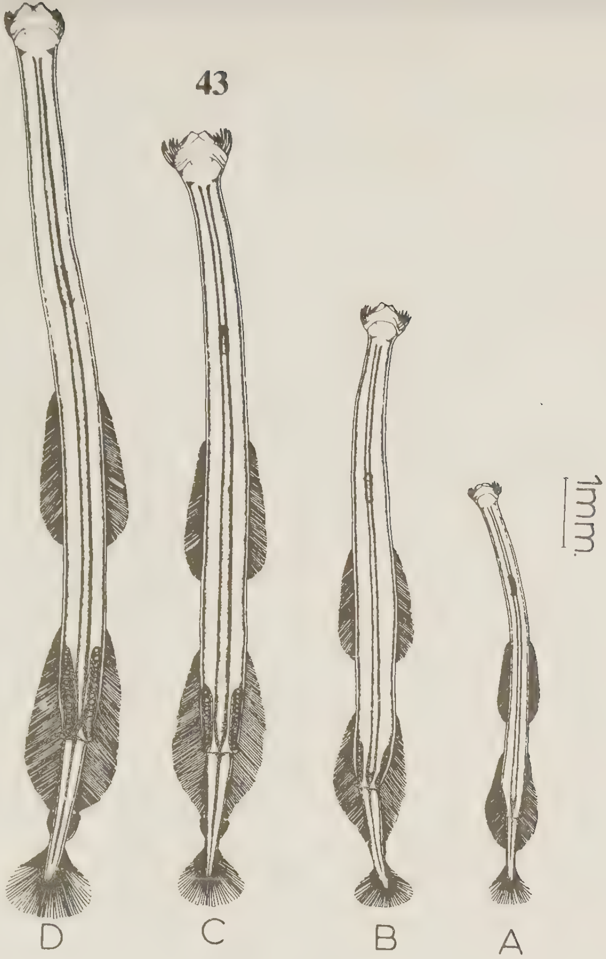

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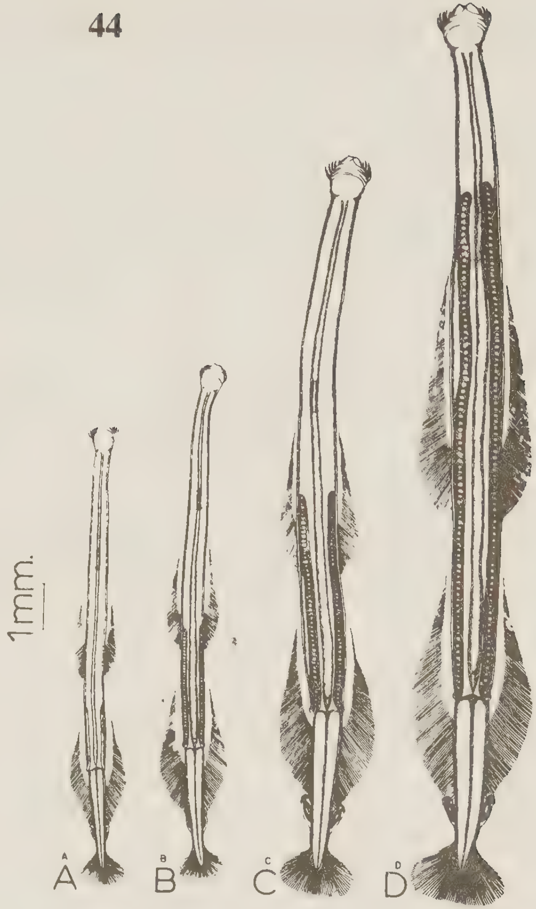

Fig. 43. Stages of maturity of *Sagitta setosa*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

Fig. 44. Four stages of maturity of *Sagitta tasmanica*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

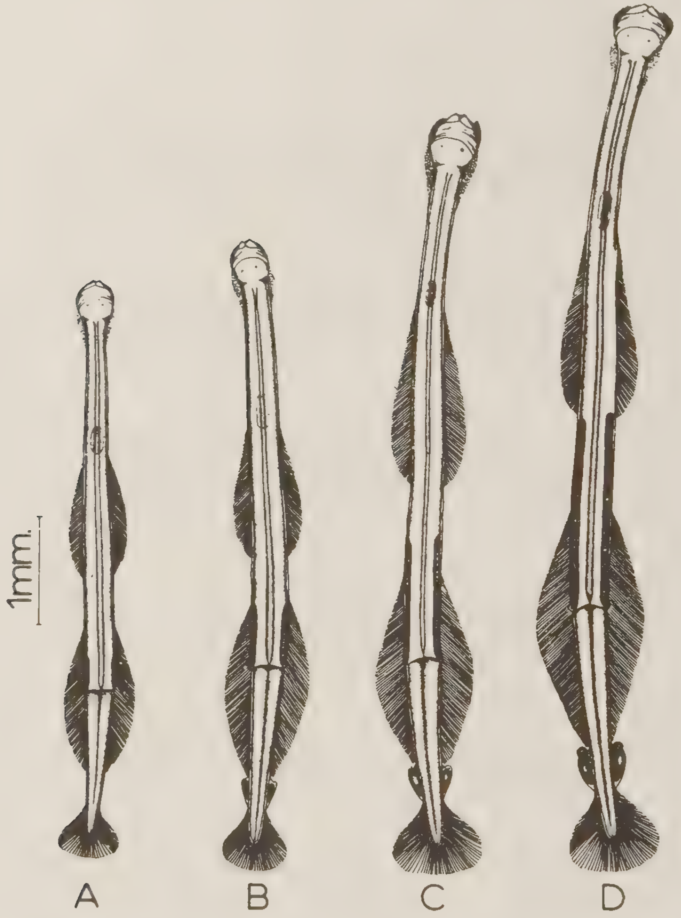

Fig. 45. Four stages of maturity of *Sagitta tenuis*. **A:** Stage I; **B:** Stage II; **C:** Stage III; **D:** Stage IV. (From Alvariño, 1969.)

B. Factors Influencing Sexual Maturity in *Sagitta scrippsae*

Sagitta scrippsae inhabits the Transition region of the North Pacific, extending into the California Current and Alaska Gyre. The population structure of *S. scrippsae* has been analysed during the monthly cruises of 1954, 1956 and 1958, and from seasonal day/night stratified collections of 1969 (see Alvariño, 1983). Four maturity stages are considered (Table 25). There are, however, exceptions to the above: specimens 50–60 mm long could appear at Stage III and specimens 31–40 mm long may reach the fully mature Stage IV. Stage I includes three size groups (up to 10 mm, 11 to 20 mm, 21 to 30 mm). Stages II, III, and IV each correspond to the next 10 mm increase in size, from 31 mm to 60 mm. Judging from the nature of the ovary, there appears to be only one 'female' maturity cycle in this species. Protandry is strong: late Stage II specimens, 39–40 mm long, may have mature seminal vesicles, but the ovaries are not mature until the animal is more than 50 mm long.

There is some evidence the testes of this species might go through several cycles of maturity in the life span of the individual, producing sperm, releasing them by copula into the seminal receptacle of another *S. scrippsae,* and starting a new cycle of sperm production to enable the animal to copulate again with another specimen.

The breeding season of chaetognaths can be determined by counting the number of individuals at Stage I, juveniles and larvae, and by comparing the percentage of mature adults to the percentage of young ones. The total number of ova produced by each individual ranges from 700 to 1,000 in *Sagitta scrippsae.* The average number of ova in mature specimens can be used to determine egg production at optimum conditions for reproduction, growth, and survival of the populations, in the species domain. There is a need for caution in that the California region is the margin of the distributional range of *S. scrippsae.*

It is obvious that the population structure of *Sagitta scrippsae* will change progressively with the southern drift of the California Current. In the northern-most part of the region, close to the main distributional area of *S. scrippsae,* the whole population structure may be represented, but the number of mature individuals will be decreasing progressively southward, until the only ones present are at Stage I. It is possible that some population replacement may occur locally. The fact that in most of the California region only Stage I specimens were observed in abundance, indicates that the conditions here may not be suitable for survival of the species, and that specimens may experience an arrest in their normal development. In the region surveyed off California, two phenomena were superimposed during the spring–summer period: the major spawning in the population and the maximum flow of the California Current which conveys the population of *S. scrippsae* southward into the California region (Alvariño, 1983).

Adults of *Sagitta scrippsae* are present all year round in the Transition region of the North Pacific (domain of the species, and area where massive reproduction takes place). In fact, in the Transition region the complete structure of the population of *S. scrippsae* is present, from newly hatched individuals (Alvariño, 1962, 1964, 1965a, b) to fully mature ones, while in the California waters young and large mature specimens were only occasionally observed, mainly at the northern part of the region (Alvariño, 1983).

The population of *Sagitta scrippsae,* observed off California during the four seasons of 1969 (Alvariño, 1983), included some young (10–20 mm), which indicates some breeding had occurred mainly during the spring and summer months. Stage I appeared all year round, and constituted 90 per cent of the population; other stages made up the rest. Some individuals, 35, 40, 41, and 45 mm long, were obtained off California in May with precociously mature female gonads (Stage IV). This may be because these individuals received optimal conditions of food and other factors, which together with high temperature permitted precocious development of their gonads. Or, it could be, as observed by Reeve (1970) in laboratory studies on *S. hispida,* simply the mistaken result of shrinkage in body length due to starvation. There seems to be a marked relation between oxygen consumption and temperature in the ecology of *Sagitta scrippsae*. Consumption of oxygen is generally relatively high in northern species (Sparck, 1936). With increase in temperature and the rise in metabolism, the need for food and oxygen reaches such a degree that the animal is likely to risk starvation.

Temperature and salinity conditions encountered by *Sagitta scrippsae* off California are similar to those found in the distributional domain of the species, as the population sinks with the waters flowing from the north. The conditions off California should be adequate for breeding and survival of the species. However, breeding took place only at random south of San Francisco. Perhaps some chemical in the waters, or the kind of food available, or both may stop the maturity process, and reduce the chances of survival of the newborn. Disappearance of fully mature animals from the California region may be due to their inability to survive under conditions adverse to the species. The result of the decimation of the population is that large mature individuals will be in small numbers, with little chances to be represented in the plankton collections.

Growth, maturity of the gonads, and production of oocytes and eggs might be related to characteristics of the food supply. *Sagitta scrippsae* devour every type of zooplankton, including fish larvae. However, both the amount and quality of available food might be critical factors. *Sagitta scrippsae,* like all chaetognaths, is incapable of storing food.

Sameoto (1973) stated that food was not a limiting factor in determination of growth and maturity of *Sagitta elegans* in Bedford Basin, Nova Scotia, and that growth and maturity were determined by the water temperature. It is generally accepted that growth rate is retarded by lack of food or unfavourable conditions in the natural habitat (Russell, 1932a), and that growth rate and maturity of the gonads are accelerated with increasing temperature. Some specimens of *Sagitta scrippsae* studied here were sexually retarded, e.g. 40 to 45 mm specimens, normally corresponding to Stage III, appeared to be at Stage I or II. Such differences in maturity of the gonads might be dependent on food and other environmental conditions that affect the physiology of the animals. Temperature may be relevant, when other factors remain constant, such as food or other undetermined environmental conditions. In this study, even though temperature encountered in the waters inhabited by the species off California was similar to or even higher than that in the range for the species in the main distributional region, gonad development did not appear directly related to this variable. Growth and sexual maturity should not have been retarded, only increased by such temperatures. However, a failure of gonad development was observed.

C. Parasitic Arrest of Gonad Development

A variety of parasites (e.g. cercaria: Hutton, 1954; nematodes: Russell, 1932a, b) have been found within the trunk cavity of chaetognaths, at times pushing the ovaries away, and Alvariño (1965a) asserts that this would adversely affect reproduction.

In *Sagitta scrippsae*, parasitized by nematodes and trematodes in the trunk cavity, the ovaries showed retarded development. Individuals, more than 40 mm long were only at Stage I of maturity. Parasitic retardation of ovarian development seen in *S. scrippsae* may be related to the paucity of nutrients in the host caused by the parasites. It may be hypothesized, from this cue, that lack of adequate food could be the factor responsible for gonad arrest normally seen in *S. scrippsae* population of the California region.

D. Adaptive Significance of Large Size and Long Life

Marine zooplankters of high latitudes develop more slowly, reach large size, and live longer than related species in warm regions. This is an adaptation of the organisms (Digby, 1954) to low temperatures. Large size and associated low growth and low metabolism may confer advantages on animals enduring periodic food shortages (McLaren, 1966).

Sagitta elegans matures in two years in the Arctic and North Canada, and in one year or less in warmer regions. The newborn, 2 mm in length, appear in the plankton during the seasonal plankton boom, when nauplii of small copepods are abundant (Dunbar, 1962). Three generations of *S. elegans* may be found in the arctic region: newborn and young, one-year-olds (adolescents), and mature two-year-olds.

The complete cycle of development of *Sagitta hispida*, 'from egg to egg', was obtained by Reeve (1970) in the laboratory. Eggs obtained from mature animals, were maintained at 22° to 24°C and 30‰ salinity, and about 3,000 larvae were produced. These larvae developed into juvenile adults in a few days.

E. Annual Cycle and Production

Sagitta crassa, from Japan Inland Sea, produces at least three generations a year: a spring–summer population born in spring and laying eggs in summer, a summer–autumn population with a three-and-a-half-month life span, and an autumn–winter population with a five-month life span (Murakami, 1959). The author thinks that a fourth generation, born in summer and laying eggs in winter, may also be present. Seasonal variations observed in abundance of larvae, adults, and breeding individuals appear to confirm the presence of such a fourth generation. The strongest and the most abundant spring–summer generation develop during the warm period, when food is abundant and the metabolism rapid; the animals reach maturity at a small size, lay eggs, and die. During cold periods, it takes longer for *S. crassa* to reach maturity as the animals grow slowly due to the low rate of metabolism. Factors, such as awailability of food, hormones or other active substances, and temperature, accelerate metabolism *vis-à-vis* sexual maturity.

While studying Chaetognatha populations in the ocean, polymodal curves could be observed: populations structures show a mixture of specimens or populations from different sources and environments converging in the region. Many authors have indicated great variations in size of specimens at the stages of maturity, without realizing that the population they were observing was a mixture of individuals of different environmental origins.

Sagitta hispida, abundant in Biscayne Bay, Florida, was studied in some detail by Reeve (1966). There is a large fluctuation in *S. hispida* population in that region, ranging from 2 per m^3 to about 80 m^3, with at least two peaks of abundance from April to June and October to November. It appears that from approximately May to September, the population remains almost static in size. The high temperature of the summer arrests the development of *S. hispida,* and the population merely survives. *S. hispida* studied experimentally in the laboratory by Reeve (1970), reached maturity in 33 days. Small larvae fed on copepod nauplii, veligers, polychaete larvae, and tintinnids. Larval stage was 0.9 to 4.0 mm long (10 to 15 days old), juvenile stage was 4.0 mm to 6.5 mm (four to eight days old), and adults ranged from 6.5 mm to more than 8.00 mm, when mature eggs were laid.

Sagitta elegans, from Bedford Basin, Nova Scotia, appears to produce two generations a year, one in the spring and another in the fall. The specimens in the population of Bedford Basin reached a maximum length of 27 mm and those of St. Margaret's Bay 32 mm (Sameoto, 1971, 1973). It appears that the fall generation of *S. elegans* constitutes 86 per cent of the total for the year, and the spring generation 14 per cent. Egg-laying begins late in May and increases subsequently as more and more copepods become available in the plankton. The decline in numbers of copepods is the result of increased predation by the newly hatched *S. elegans* larvae. In the Plymouth region (Great Britain), *S. elegans* presented a seasonal size difference: 19.5 to 20.0 mm in May, 13.4 to 14.5 mm in June, 13 mm in July, 10.0 to 10.5 mm in September, 12.0 to 12.5 mm in February, and 16 mm in April–May (Russell, 1932a). Those laying eggs in February were born under higher temperature conditions than those laying eggs in September. Consequently, those developing under high temperature reached maturity early in life and at small size. It is probably also that size attained is conditioned by the food supply. Clarke *et al.* (1943) observed that the *S. elegans* population in the Georges Bank region ranged from 16 to 30 mm. Temperature in the U.S. North Atlantic is similar to that off Plymouth (England). The difference in size of the specimens here is explained by the flow of *S. elegans* from the northern population into the Banks via the Labrador current. Therefore, in the U.S. North Atlantic, there is mixture of indigenous population of *S. elegans* and that from the Canadian waters (Alvariño, 1965a). No such mixing of the populations takes place in the British waters.

Russell (1933b) indicates that *Sagitta elegans* in the English Channel shows two periods of maximum abundance: February and July–September, or March and August–September. *Sagitta setosa* also presented two periods of maximum abundance: April and August–November, or March and August–November. *S. elegans* and *S. setosa* populations reached a maximum in spring and summer, and a minimum during the winter months (Russell, 1932a, b; 1933a, b).

IV. ECOLOGICAL ASPECTS OF REPRODUCTIVE CYCLES

Much work on reproductive cycles of marine invertebrates has been directed towards elucidation of the exogenous proximate factors synchronizing the cycles. However, it should be remembered that the timing of the various models of reproduction is a response to selection pressure, a reflection of environmental conditions favourable for a successful reproduction.

The breeding cycles are so regulated and synchronized with the environment that the larvae hatch at a time when temperature, salinity, and food conditions are favourable. In temperate seas most species breed in spring and summer, when the necessary planktonic food for the larvae is available. Demonstration by Barnes (1957) that diatom blooms induce barnacles to release their larvae is a good example for this kind of close adaptative synchrony.

Conditions in polar seas (Thorson, 1946, 1950) are decidedly unfavourable for planktonic larvae. Low temperature slows down development and reduces the period during which phytoplankton and other foods are available. Most polar species apparently respond to these circumstances by brooding their young (e.g. *Eukrohnia*), and thus avoid unfavourable food conditions during the critical period of larva hatching. In the tropics, where food and other conditions are almost uniformly favourable throughout the year, breeding is more or less continuous (Thorson, 1950). There is scanty knowledge of the ultimate causes of breeding cycles in marine animals. At present, human activities are drastically changing many areas of the world, including the sea, and it is important to ascertain the environmental factors critical to the success of reproduction in the different marine animals.

A. Temperature

Temperature changes in the sea may influence the reproductive activity of marine animals. Sea temperatures often vary rhythmically through the year, not as drastically as on land. Changes in sea temperature might therefore provide marine animals with reliable clues to seasonal changes, and may serve to synchronize their reproduction. Many reviews on the subject are available (Gunter, 1957; Kinne, 1963, 1970). Each species may have a critical breeding temperature (Orton, 1920) which should occur before reproductive activities develop. Species mature at different temperature ranges within their distributional region, and the above statement should apply to the various populations corresponding to the species. How precisely temperature influences various aspects of reproduction, such as gametogenesis, spawning, and breeding, is not known. Receptors in the animals initiate these events, but they have not been identified. Temperature changes influence both feeding activity and general metabolic processes, and consequently influence reproduction by affecting the utilization of nutrients available.

B. Day Length

Day length (amount of light) could be a factor in synchronizing biological events, because it is constant for the same latitude and time of the year. The farther the localities from the equator, the greater the seasonal difference in day length; and in consequence this would be a clue to the animal to determine the season. In the equatorial region, day length is homogeneous through the year, and reproduction is continuous, not restricted to a season or period. However, gametogenesis is generally triggered by hormones, the production of which is influenced by extrinsic factors. It is well known that, under light control, animals produce hormonal substances that trigger the reproductive process (Wells, 1960; see also Brahmachary, Volume IV, Part A, p. 336). In this connection, there is need to consider, in Chaetognatha, the size of the eyes and the thickness and extension of the pigment in them (directly related to the amount of light in the habitat). Deep-water chaetognaths have large ommatidia and only a small amount of pigment, which will permit the bright reception of light. When breeding takes place in the dark, higher temperature is required than when some illumination is provided each day, suggesting that light has some stimulatory influence upon gametogenesis (Barnes, 1963).

C. Salinity

Fluctuations in salinity are not likely to affect reproduction in chaetognaths. This is because salinity changes are not sharp in most regions, except in shallow waters, estuaries and coastal lagoons. Prolonged changes in salinity only occur during rains, flooding of rivers, strong evaporation during dry seasons, and strong tides. Along the coast of India (Cochin backwater), chaetognaths reproduce ten times more frequently than normal during the post-monsoon period in the boundary area between backwaters and coastal waters, an enriched region providing adequate setting for successful reproduction (Nair, 1974). However, in this case, the factor responsible for the productivity may not be salinity, but food concentration.

D. Food

Abundance of food may be important in the regulation of gametogenesis. Seasonal plankton blooms might regulate gametogenesis by making available adequate supplies of food at certain times. This may be the case in temperate regions, particularly the polar seas, where plant production occurs mainly in summer. At least the spring and summer breeding periods of temperate and polar species are correlated to the increase in plant production (Pearse, 1966).

Prolonged starvation, started early in the season, prevents gametogenesis and fertilization in cirripedes (Barnes and Barnes, 1967). Chaetognatha do not store food, as already mentioned (Section III B) and, therefore, are in need of continuous food supply for survival. Gametogenesis seems to be sensitive to levels of reserve nutrients, which, in turn, are dependent upon seasonal fluctuations in quantity and quality of food supplies. In chaetognaths developing at locations of low food supply close to starvation levels, the development of gonads and maturity is arrested; ova may be reabsorbed and only a few elongated thin ova are present in the ovaries.

Chemicals related to changes in quality of nutrient supplies, such as trace metabolites in the food, might serve as synchronizers of reproduction. The chemical composition of many planktonic organisms varies seasonally (Wort, 1955; Jensen, 1969; Rao, 1969) and qualitative nutrient changes may be detected by feeding animals. These changes would serve as proximate exogenous regulators of reproduction. *Sagitta scrippsae* inhabiting the North Pacific Transition region do not reproduce off California (Section III B) due probably to lack of a certain substance in the food supply necessary to trigger maturity (Alvariño, 1962, 1983, and other personal data).

V. CHEMICAL SIGNALS AND MALE RECOGNITION

Metabolites may leak (Giese and Pearse, 1973) from plants and animals to be detected by other animals as exogenous clues, and influence the reproductive activities of other members of the same species or other animals (pheromones). Chemical releases during spawning often stimulate other members of the same or other species, leading to synchronous epidemic spawning (Lucas, 1961; Alvariño, 1989; Hardege *et al.*, 1991).

Chemical signals play an important role in inter- and intraspecific communication. Aquatic animals depend on chemical and mechanical receptors more than on the visual sensory equipment (Mackie and Grant, 1974). Many volatile and odoriferous sex attractants and other pheromones have been isolated in arthropods (see e.g. Hinsch, this volume). In marine animals pheromones have been identified, but, in general, these water-soluble signals are only in trace amounts, and the isolation of pure pheromone is a difficult task. The nuptial-dance-coordinating sex pheromone of some epitokous heteronereid polychaetes is 5-methyl-3-heptanone (see Hardege *et al.*, 1991), a pheromone also found in insects. Chemical interactions in animals of different species deal with chemicals secreted by one species that affect the population of another species (Mackie and Grant, 1974).

Chemical information may be basic in survival of the species. Organisms are dependent on chemicals in their activities of feeding, reproduction, and protection. Living organisms, through metabolic processes, release substances to the environment, chemicals which might serve as clues for predators and partners. Receptor mechanisms in chaetognaths are the corona ciliata and sensory epidermal tufts, and the substances released are specific. Communication for reproduction is necessary in aquatic organisms, which could be specific chemical signals triggering the mating process. The dissemination of the signal and the distance reached have not been determined.

The chemoreceptor cells in the nervous system are directly associated with the secondary neurones, acting as conduction pathways to the central nervous system. The Chaetognatha have a fairly well-developed nervous system, with the unique corona ciliata, a chemoreceptor.

'Female-substances' may induce the passage of sperm into the seminal receptacle annex to the oviduct. In chaetognaths, the ova seem to activate sperm maturation in the seminal receptacles, and the sperm deposited therein, in turn, seem to activate oocyte development. I have never seen chaetognaths with full mature ovaries and no sperm in the seminal receptacle: the absence of sperm in the seminal receptacle may, in fact, arrest the development of the female gonads. This observation also illustrates that mating is an indispensable prerequisite for successful reproduction in chaetognaths: sperm directly from the seminal vesicle are not adequately mature to fertilize the ovum. It is not clear whether a process of sperm capacitation is involved here. More work is needed in this area.

REFERENCES

Alvariño, A. (1962). 'Two new Pacific chaetognaths; their distribution and relationship to allied species', *Bull. Scripps Inst. Oceanogr. Univ. California*, **8**(1), 1–50.

Alvariño, A. (1963). 'Epiplanktonic Chaetognatha of the Sea of Cortes (Quetognatos epiplanctónicos del Mar de Cortés)', *Rev. Soc. Mex. Hist. Nat.*, **24**, 97–203; *Contrib. Scripps Inst. Oceanogr.*, **34**(1646), 645–752.

Alvariño, A. (1964). 'Bathymetric distribution of Chaetognaths', *Pac. Sci.*, **18**(1), 64–82; *Contrib. Scripps Inst. Oceanogr.*, **34**(1616), 39–57.

Alvariño, A. (1965a). 'Chaetognaths', *Oceanogr. mar. Biol. Ann. Rev.*, **3**, 115–194.

Alvariño, A. (1965b). 'Distributional atlas of Chaetognatha in the California Current Region during the CalCOFI monthly cruises of 1954 and 1958', *Calif. Coop. Oceanic Fish. Invest. Atlas*, 3(I–XIII), 1–291.

Alvariño, A. (1967). 'The Chaetognatha of the NAGA Expedition (1959–1961) in the South China Sea and the Gulf of Thailand. Part I. Systematics', *Scientific Results Mar. Invest. South China Sea and the Gulf of Thailand*, 4(2), 1–197.

Alvariño, A. (1968). 'Egg pouches and other reproductive structures in pelagic Chaetognatha', *Pac. Sci.*, **22**(4), 488–492; *Contrib, Scripps Inst. Oceanogr.*, **38**(2349), 554–558.

Alvarino, A. (1969). 'Atlantic Chaetognatha. Distribution and essential notes of Systematics (Los Quetognatos del Atlántico. Distribution y notas esenciales de Sistematica)', *Trab. Inst. Español. Oceanogr.*, **37**, 1–290.

Alvariño, A. (1983). 'The depth distribution, relative abundance and structure of the population of the Chaetognatha *Sagitta scrippsae* Alvariño 1962, in the California Current off California and Baja California', *Anales instituto Ciencias del Mar y Limnologia Universidad Nacional Autonoma de Mexico*, **10**(1), 47–84.

Alvariño, A. (1989). 'Abundance of zooplankton species, females and males, eggs and larvae of holoplanktonic species. Zooplankton assemblages and changes in the zooplankton communities related to *Engraulis mordax* spawning and survival of the larvae', *Memorias do III Encontro Brasileiro de Plancton*, December, **1988**, pp. 63–149.

Barnes, H. (1957). 'Processes of restoration of synchronization in marine ecology: the spring diatom increases and the "spawning" of the common barnacle, *Balanus balanoides* (L)', *Ann. Biol.*, **33**, 67–85.

Barnes, H. (1963). 'Light, temperature and the breeding of *Balanus balanoides* (L.)', *J. mar. biol. Ass. U.K.*, **43**(3), 717–727.

Barnes, H., and Barnes, M. (1967). 'The effect of starvation and feeding in the time of production of egg masses in the Boreo-arctic cirriped, *Balanus balanoides* (L.)', *J. exp. mar. Biol. Ecol.*, **1,** 1–6.

Clarke, G.L., Pierce, E.L., and Bumpus, D.F. (1943). 'The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to the hydrographical conditions', *Biol. Bull.*, **85,** 201–226.

Colman, J.S. (1959). 'The ROSURA Expedition, 1937–38, Chaetognatha', *Bull. Brit. Mus. Nat. Hist. Zool.*, **5**(8), 219–253.

David, P.M. (1955). 'The distribution of *Sagitta gazellae* Ritter-Zahony', *Discovery Rept.*, **27,** 235–278.

Digby, P.S.B. (1954). 'The biology of the marine planktonic copepods of Scoresby Sound, East Greenland', *J. Anim. Ecol.*, **23,** 298–338.

Dunbar, M.J. (1962). 'The life cycle of *Sagitta elegans* in Arctic and Subarctic seas and the modifying effects of hydrographic differences in the environment', *J. Mar. Res.*, **20,** 76–91.

Ghirardelli, E. (1961a). 'Istologia e citologia degli stadi di maturita nei Chetognati', *Bol. Pesca Piscic. Idrobiol.*, **15**(1), 3–16.

Ghirardelli, E. (1961b). 'Osservazioni citometriche ed istofotometriche sugli ovociti di, *Spadella cephaloptera*', *Boll. Zool.*, **28**(2), 379–388.

Giese, A.C., and Pearse, J.S. (1973) (Eds). *Reproduction of Marine Invertebrates*, Vol. 1, Academic Press, New York, pp. 1–48.

Gunter, G. (1957). 'Temperature', in *Treatise in Marine Ecology and Palaeo-ecology*, Vol. 1 (Ed. J.W. Hedgpeth), Mem. 67, Geol. Soc. Amer., pp. 159–184.

Hardege, J.D., Bartels-Hardege, H., and Zeeck, E. (1991). 'Volatile compound from the coelomic fluid of *Nereis succinea:* biological activity as sex pheromone', *Inv. Reprod. Dev.*, **19,** 83–85.

Hutton, R.F. (1954). '*Metacercaria owreae* n. sp., an unusual Trematode larva from the Florida Current chaetognaths', *Bull. mar. Sci. Gulf. Carib.*, **4,** 104–109.

Jensen, A. (1969). 'Seasonal variations in the content of individual tocopherols in *Ascophyllum nodosum, Pelvetia canaliculata* and *Fucus serratus* (Phaeophyceae)', *Proc. 5th Int. Seaweed Symp.*, pp. 493–500.

Kinne, O. (1963). 'The effects of temperature and salinity on marine and brackish water animals. Temperature', *Oceanogr. mar. Biol. Ann. Rev.*, **1,** 301–340.

Kinne, O. (1970). 'Temperature, animals, invertebrates', in *Marine Ecology*, Vol. 1(1) (Ed. O. Kinne), John Wiley, New York, pp. 407–514.

Kramp, P.L. (1917). 'Chaetognatha collected by the Tjalfe Expedition to the West Coast of Greenland in 1908 and 1909', *Vid. Medd. Dansk Naturh. Foren.*, **69,** 17–55.

Kramp, P.L. (1939). 'The Godthaab Expedition 1928, Chaetognatha', *Medd. Grónland Komm. Vid. unders. Grønland*, **80**(5), 1–38.

Lucas, C.E. (1961). 'External metabolites in the sea', in *Papers in Marine Biology and Oceanography* (Ed. M. Sears), Pergamon Press, New York, pp. 139–148.

Mackie, A.M., and Grant, P.T. (1974). 'Interspecies and intraspecies chemoreception by marine invertebrates', in *Chemoreception in Marine Organisms* (Eds. P.T. Grant and A.M. Mackie), Academic Press, London, pp. 105–141.

McLaren, I.A. (1966). 'Adaptative significance of large size and long life of the chaetognath *Sagitta elegans* in the Arctic', *Ecology*, **47,** 852–855.

Murakami, A. (1959). 'Marine biological study on the planktonic chaetognaths in the Seto Inland Sea', *Bull. Naikai Reg. Fish. Res. Lab.*, **12,** 1–186.

Nair, V.R. (1974). 'Distribution of chaetognaths along the salinity gradient in Cochin backwater, an estuary connected to the Arabian Sea', *J. mar. biol. Ass. India*, **16**(3), 721–730.

Orton, J.H. (1920). 'Sea-temperature, breeding and distribution of marine animals', *J. mar. biol. Ass. U.K.*, **12,** 339–366.

Pearse, J.S. (1966). 'Antarctic asteroid *Odontaster validus:* instance of reproductive periodicity', *Science*, **152,** 1763–1764.

Piyakarnchana, T. (1965). 'The plankton community in the Southern part of Kaneohe Bay, Oahu, with the special emphasis on the distribution, breeding season and population', Ph.D. thesis, University of Hawaii, pp. 1–193.

Rao, M.U. (1969). 'Seasonal variations in growth, alginic acid and manitol contents of *Sargasso wightii* and *Turbinaria conpides* from the Gulf of Mannar, India', *Proc. 5th Int. Seaweed Symp.*, pp. 579–584.

Reeve, M.R. (1966). 'Observations on the biology of a chaetognath', in *Some Contemporary Studies in Marine Science* (Ed. H. Barnes), George Allen and Unwin, London, pp. 613–630.

Reeve, M.R. (1970). 'Complete cycle of development of a pelagic chaetognath in culture', *Nature, Lond.*, **227**, 381.

Russell, F.S. (1932a). 'On the biology of *Sagitta.* The breeding and growth of *Sagitta elegans* Verrill in the Plymouth Area', *J. mar. biol. Ass. U.K.*, **18,** 131–145.

Russell, F.S. (1932b). 'On the biology of *Sagitta.* II. The breeding and growth of *Sagitta setosa* J. Muller in the Plymouth area, 1930–31, with a comparison with that of *S. elegans* Verrill', *J. mar. biol. Ass. U.K.*, **18,** 147–160.

Russell, F.S. (1933a). 'On the biology of *Sagitta.* III. A further observation on the growth and breeding of *Sagitta setosa* in the Plymouth area', *J. mar. biol. Ass. U.K.*, **18,** 155–158.

Russell, F.S. (1933b). 'On the biology of *Sagitta.* IV. Observations on the natural history of *Sagitta elegans* Verrill and *Sagitta setosa* J. Muller in the Plymouth area', *J. mar. biol. Ass. U.K.*, **18,** 559–574.

Sameoto, D.D. (1971). 'Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia', *J. Fish. Res. Board, Can.*, **28** (7), 971–985.

Sameoto, D.D. (1973). 'Annual life cycle and production of the chaetognatha *Sagitta elegans* in Bedford Basin, Nova Scotia', *J. Fish. Res. Board, Can.*, **30** (3), 333–344.

Sparck, R. (1936). 'Relation between metabolism and temperature in marine Lamellibranches', *Danske Vidensk. Selskab Copenhagen Biologiske Medd.*, **13,** 1–27.

Thomson, J.M. (1947). 'The chaetognath of southeastern Australia', *Bull. Coun. sci. indus. Res. Melbourne,* **222,** 1–43.

Thorson, G. (1946). 'Reproduction and larval development, growth and metabolism of Arctic marine bottom invertebrates', *Meddr. Grønland,* **100** (6), 1–155.

Thorson, G. (1950). 'Reproductive and larval ecology of marine bottom invertebrates', *Biol. Rev.*, **25,** 1–45.

Wells, M.J. (1960). 'Optic glands and the ovary of Octopus', *Symp. zool. Soc. London,* **2,** 87–107.

Wort, D.J. (1955). 'The seasonal variation in chemical composition of *Macrocystis integrifolia* and *Nereocystis luctkeana* in British Columbia waters', *Can. J. Bot.*, **33,** 323–340.

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Global Climate Change and Intensification of Coastal Ocean Upwelling

ANDREW BAKUN

A mechanism exists whereby global greenhouse warming could, by intensifying the alongshore wind stress on the ocean surface, lead to acceleration of coastal upwelling. Evidence from several different regions suggests that the major coastal upwelling systems of the world have been growing in upwelling intensity as greenhouse gases have accumulated in the earth's atmosphere. Thus the cool foggy summer conditions that typify the coastlands of northern California and other similar upwelling regions might, under global warming, become even more pronounced. Effects of enhanced upwelling on the marine ecosystem are uncertain but potentially dramatic.

THE COASTAL OCEAN OFF THE WESTERN United States is a classic wind-driven coastal upwelling system (*1*, *2*). During the warmer seasons of the year, strong northerly and northwesterly winds induce offshore transport of surface waters. Upwelling of cool, nutrient-enriched water from depth (Fig. 1) balances the resulting loss of surface water near the coast and infuses essential plant nutrients to the surface layers of the ocean. Rich phytoplankton growth supports an abundant trophic pyramid, including valuable fishery resources and important seabird and marine mammal populations (*3*). Cooling and stabilization of the onshore air flow by contact with the upwelled surface waters leads to the cool summer climate of the adjacent coastlands (*4*). Similar upwelling systems occur in the other major subtropical eastern ocean boundary regions; examples are the Canary current system off the Iberian Peninsula and northwestern Africa, the Benguela current system off southwestern Africa, and the Peru current system off western South America. Upwelling in all of these regions tends to be highly seasonal in temperate latitudes, where it peaks in the spring-summer, but tends toward year-round continuity in the more tropical portions (*1*).

The vigorous alongshore wind that drives coastal upwelling in these systems is maintained in part by a strong atmospheric pressure gradient between a thermal low-pressure cell that develops over the heated land mass and the higher barometric pressure over the cooler ocean (*5*). Because of the large-scale atmospheric subsidence occurring in the eastern limbs of the subtropical gyres, and also because of the stabilized, dehumidified onshore air flow, the areas of these coastlands inland of the direct influence of coastal stratus and fog are characterized during the upwelling seasons by dry Mediterranean-type (or desert) climates and clear atmospheric conditions (*4*). The clear conditions lead to strong daytime heating by short-wave solar radiation, particularly in interior valleys such as the Central Valley of California, and rapid nighttime, long-wave radiative cooling.

Recent decades have seen a substantial build-up of CO_2 and other greenhouse gases in the earth's atmosphere (*6*). Resulting inhibition of nighttime cooling and enhancement of daytime heating should lead to intensification of the continental thermal lows adjacent to upwelling regions. This intensification would be reflected in increased onshore-offshore atmospheric pressure gradients, intensified alongshore winds, and accelerated coastal upwelling circulations (Fig. 1). As a positive feedback, the cooling of the ocean surface that results might locally intensify the low-altitude barometric highs at the oceanic sides of the onshore-offshore pressure gradients.

No routine observations of actual rate of upwelling are available. Accordingly, a coastal upwelling index based on an estimate

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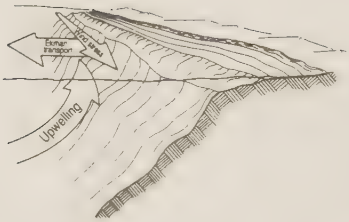

Fig. 1. A conceptual diagram of the coastal upwelling process [modified from (*6*)]. The coast is represented in cutaway view and the ocean is to the left. Offshore transport in the surface Ekman layer driven by the alongshore stress of the wind on the sea surface is replaced by upwelling from depth.

of the alongshore wind stress (that is, the driving force for upwelling) has been used to indicate variations of intensity of upwelling in the California Current region (*5*, *7*). Wind observations reported by ships at sea tend to be irregularly distributed in time and space. In order to produce homogeneous time series, the upwelling index computations are based on analyzed fields wherein the geostrophic constraint is employed to incorporate data on both wind and barometric pressure, and information is spread in time and space to fill data voids and to detect erroneous reports (*8*).

The highest intensity core of the California Current upwelling system is situated in the Point Arena–Cape Mendocino region near 39°N (*1*). The equatorward alongshore wind stress during the spring-summer upwelling season, derived on the basis of the upwelling index methodology, has apparently intensified in the 30-year period 1945 to 1975 (Fig. 2A). Since 1975 the stress values have trended back toward the mean for the entire (~40-year) period. Actually, the period since 1975 has been one of anomalously warm conditions in the ocean off California (*9*); whether warm ocean conditions could have affected the onshore-offshore pressure gradient by lessening the relative barometric high at the oceanic end of the gradient is unclear. In any case, substantial, natural interyear and interdecadal variability should be superimposed on any trends related to climatic warming. Certainly, the trend line fitted to the values in Fig. 2A indicates a trend toward substantially increased southward wind stress off the coast of northern California, even over the entire 1946 to 1988 period.

Because of the spatial spreading of information in the analysis procedures, the upwelling index series at different locations in the same region do not represent independent verifications of the trend. However, the index series do reflect significant spatial differences in the California current region (*5*, *7*). All of the spring-summer series for this region (Table 1) show a trend toward increased intensity of upwelling-producing wind stress, except for the series located at 24°N and 27°N. These two locations are off Baja California, where the waters of the Gulf of California rather than continental land surface occupy the interior and where therefore the proposed mechanism would be ineffective.

Off the Iberian Peninsula in the northeastern Atlantic Ocean, a 35-year trend toward increased wind stress during the spring to summer upwelling season (Fig. 2B and Table 1) has been reported (*10*). Farther south in the Canary current region (southern Morocco; 28°N), annual mean values of upwelling are available for the period 1946 to 1981 (*11*). In this area, coastal upwelling, while peaking in the summer, tends to persist throughout the year (*12*). Therefore, the use of the mean values, although not ideal, appears acceptable. Again, the general increasing trend is pronounced (Fig. 2C and Table 1).

The upwelling system off Peru presents an extreme tropical case; coastal upwelling continues throughout the year and is actually somewhat more intense in austral winter than in summer (*1*). Because of the low-latitude location and correspondingly weakened geostrophic constraint, upwelling index computations are not appropriate.

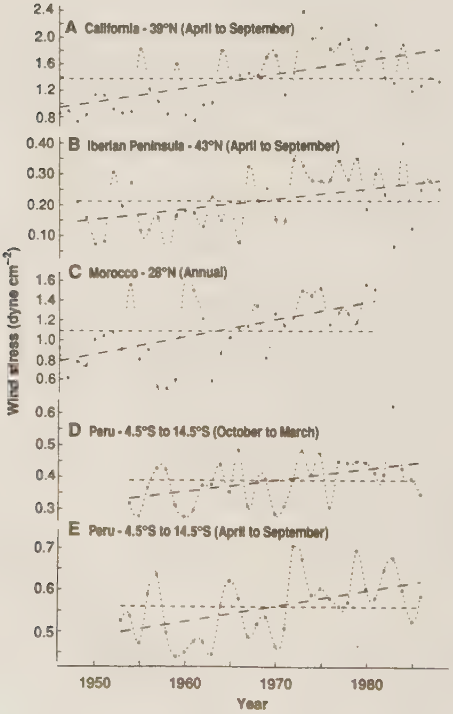

Fig. 2. Within-year averages of monthly estimates of alongshore wind stress off (**A**) California, (**B**) the Iberian Peninsula, (**C**) Morocco, and (**D** and **E**) Peru (in D, each mean value for October to March is assigned to the year in which the January to March portion falls). Short dashes indicate the long-term mean of each series. Longer dashes indicate the linear trend fitted by the method of least squares.

Table 1. Location calendar months incorporated in annual data, slope of the linear trend [significance: * = $P < 0.05$; ** = $P < 0.01$; (*30*)], and standard error of that slope, for averages of monthly alongshore wind stress series.

Latitude or area	Months	Slope (dyne cm^{-2} year^{-1})	Standard error
Upwelling index, northeastern Pacific			
48°N	4 to 9	0.0051**	0.0012
45°N	4 to 9	0.0011	0.0018
42°N	4 to 9	0.0033	0.0032
39°N	4 to 9	0.0206**	0.0044
36°N	4 to 9	0.0102*	0.0046
33°N	4 to 9	0.0136**	0.0050
30°N	4 to 9	0.0022	0.0030
27°N	4 to 9	−0.0041	0.0027
24°N	4 to 9	−0.0021	0.0021
Upwelling index, northeastern Atlantic			
43°N	4 to 9	0.0033**	0.0011
37°N	4 to 9	0.0051**	0.0018
28°N	1 to 12	0.0174**	0.0044
Ship reports, northeastern Atlantic (Fig. 4)			
Area A	4 to 9	0.0101**	0.0024
Area B	4 to 9	0.0048*	0.0022
Area C	4 to 9	0.0060**	0.0018
Area D	4 to 9	0.0064**	0.0016
Ship reports, southeastern Pacific			
Peru	4 to 9	0.0038**	0.0011
Peru	10 to 3	0.0035**	0.0012

Here, wind stress estimates based on individual wind reports from ships at sea have been averaged by month over an area of coastal ocean between 4.5°S and 14.5°S latitudes (*13, 14*). The long-term increasing trend in equatorward alongshore wind stress is not only clearly evident during the spring to summer half of the year (Fig. 2D), but also during fail to winter (Fig. 2E).

The procedures used to derive the various time series from the available data bases have been consistently applied over the entire record. The analyzed data fields forming the data base for the upwelling index computations (*5*) have been routinely produced throughout the record period in support of weather forecasting activities. Because of the extended period of assembly of these data, one wonders if artificial inhomogeneities could have crept in to produce the indicated trend (such as the transition from subjective hand analysis to objective computer analysis, altered data distributions due to changes in shipping routes, or establishment of new coastal reporting stations in data-poor areas). Because the analysis procedures act to spread available information in time and space, one cannot look to upwelling index series computed at nearby locations for independent corroborations.

The area off Spain and Portugal is much higher in maritime data density than the other major eastern ocean upwelling regions, including California (*1*). Here, four strictly independent (sharing no data) series of monthly means of wind stress estimates have been constructed from ship reports available in each of four adjacent 5° latitude by 5° longitude quadrangles (Fig. 3). Although details of the shorter scale interyear variability appear somewhat different among the four series, they all corroborate (Fig. 4 and Table 1) the increasing trend indicated in Fig. 2B.

Thus data from widely separated areas around the world suggest that the equatorward alongshore wind stress that drives coastal upwelling has been increasing during the respective upwelling seasons of the past 40 years. In seasons when upwelling is weak or absent, no consistent pattern of increasing equatorward stress is apparent (for example, off California the slopes of the trend lines for the series of October to March means are weakly negative; off the Iberian Peninsula the fall-winter series exhibit a mixture of weakly positive and weakly negative trends). Thus the increasing trend in equatorward stress is observed only during the upwelling seasons. These are the only seasons during which thermal lows in surface atmospheric pressure develop over the adjacent land mass and therefore in which the hypothesized greenhouse mechanism could operate.

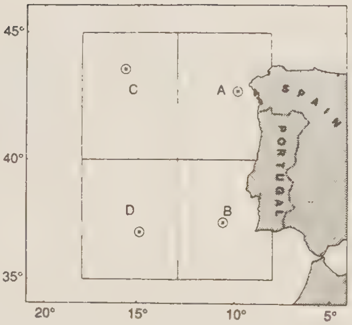

Fig. 3. Four 5° by 5° quadrangles (areas labeled A, B, C, and D) off the Iberian Peninsula in which sea surface wind stress estimates based on maritime wind reports were summarized to produce monthly time series shown in Fig. 4. The mean latitude and longitude of the reports available in each of the areas over the period 1948 to 1979 is marked by an "x" surrounded by a small circle.

When the various series are differenced, effectively removing the linear trends, significant interregional correlation among the time series vanishes. Evidently, the only feature shared among regions is the long-term trend. Other known types of global teleconnections, such as El Niño–Southern Oscillation, are known to be evident in shorter period components of interannual variability. The substantial shorter period interannual variability evident in the time series (Fig. 2) is apparently not shared among regions to any significant degree. A greenhouse mechanism is consistent with the simple monotonically increasing trend that corresponds to the observed interregional pattern. Moreover, simulations of increased atmospheric CO_2 with general circulation models suggest that southward wind stress will increase in the spring and summer off northern California (*15*).

Intensification of coastal upwelling along subtropical and tropical eastern ocean boundaries would have important consequences. Evidently, with increased global warming, the coastal surface waters in these regions could cool relative to the surfaces of either the continental land mass on one side or the ocean interior on the other. With greater temperature contrast at the land-sea boundary, summer sea breezes would tend to be enhanced. Cool, foggy, summer conditions at the coast could become even more pronounced and wind flow through passes in coastal mountain ranges toward the heated interior valleys could strengthen. The onshore air flow might become even more stable and less humid because of enhanced heat loss to the relatively cool ocean surface; thus the coastal zone inland of the fog zone might become even more arid during upwelling seasons.

Effects on the marine ecosystem are more difficult to gauge. Short-term climatic warmings, associated with intense El Niño episodes, have recently occurred in the Peru (*14*) and California (*20*) systems. But the specific dynamics underlying El Niño (*17*) are most likely not identical to those controlling effects of climate warming. Moreover the distribution of biological populations, as well as their abundance, appear often to be more related to the dynamic physical processes that control various patterns in the ecosystem (*18, 19*) than to direct effects of temperature itself. For example, recent empirical results (*20*) indicate that reproductive success of pelagic fishes in upwelling regions depends on the winds being neither so weak that there is insufficient upwelling to enrich the trophic pyramid nor so strong that turbulent mixing of the water column prevents maintenance of fine-scale concentrations of minute food organisms essential to larval survival.

In projecting direct physiological effects of climatic warming on organisms, a first inclination might be to merely increment present characteristic isotherm patterns and to predict changes in biological distributions according to the resulting translocation of

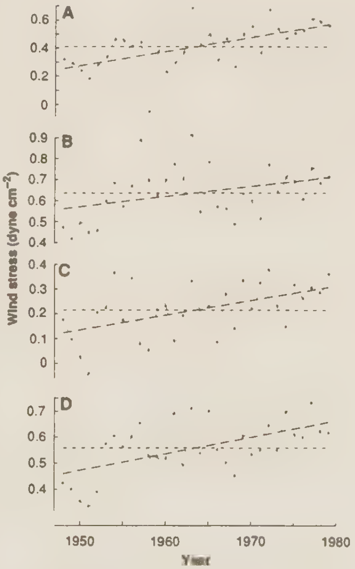

Fig. 4. Six-month (April to September) averages of monthly estimates of alongshore wind stress produced from ship reports within the four areas (A, B, C, and D) shown in Fig. 3. Short dashes indicate the long-term mean of the series. Longer dashes indicate the linear trend fitted by the method of least squares.

temperature ranges. Clearly, there are problems with such a procedure. Also, care must be taken in using evidence from past warm epochs, where various causal aspects of the warming have been somewhat different, to predict the effects of greenhouse warming on the ocean ecosystem. The dynamic ocean processes that determine the temperature distributions could be fundamentally altered.

In the absence of counteracting effects (*21*), intensified upwelling would tend to enhance primary organic production in these systems. But whether this increased primary production would be channeled to trophic components that society particularly values is unclear. There has been little clear demonstration that increased primary production actually promotes reproductive success and population growth of commercial fishes (*19, 22*). For example, increased production might be channeled to the mesopelagic fish communities that are diffused over wide areas and thereby largely lost from the neritic ecosystem. In addition, increased organic production might cause large areas of these systems to become anoxic at depth (*23*) and thereby promote sedimentation of unoxidized organic matter on the sea floor. In any case, if primary production increases, the rate at which carbon is sequestered beneath the ocean thermocline should likewise increase, and thus the rate of buildup of CO_2 in the atmosphere should be reduced.

If greenhouse warming leads to less global temperature contrast between tropical and polar regions, ocean basin–scale atmospheric and ocean circulations might slow down (*24*). However, as this example indicates, there is a competing tendency toward intensification where oceanic-continental temperature contrasts are involved. Many of the consequences of global climate change to marine ecosystems and also to marine-influenced terrestrial systems could depend on the relative importance, in each local situation, of these competing effects.

REFERENCES AND NOTES

1. R. H. Parrish, A. Bakun, D. M. Husby, C. S. Nelson, in (*2*), pp. 731–777.
2. G. D. Sharp and J. Csirke, Eds., *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources* (*Fish. Rep. 291*, Food and Agriculture Organization of the United Nations, Rome, 1983).
3. J. H. Ryther, *Science* **166**, 72 (1969); D. Cushing, *Fish. Tech. Pap. 84* (Food and Agriculture Organization of the United Nations, Rome, 1969).
4. G. T. Trewartha, *An Introduction to Climate* (McGraw-Hill, New York, 1968).
5. A. Bakun, *NOAA Tech. Rep. NMFS SSRF671* (1973).
6. V. Ramanathan, *Science* **240**, 293 (1988).
7. J. E. Mason and A. Bakun, *NOAA Tech. Memo. NMFS-SWFC67* (1986).
8. M. M. Holl and B. R. Mendenhall, *Fleet Numeric. Weather Cent. Tech. Note 72-2* (FNOC, Monterey, CA, 1972).
9. D. A. Cole and D. R. McLain, *NOAA Tech. Memo. NMFS-SWFC125* (1989).
10. W. S. Wooster, in preparation; R. R. Dickson, P. M. Kelly, J. M. Colebrook, W. S. Wooster, D. H. Cushing, *J. Plankton Res.* **10**, 151 (1986).
11. H. Belvèze and K. Erzini, in (*2*).
12. W. S. Wooster, A. Bakun, D. R. McLain, *J. Mar. Res.* **34**, 131 (1976).
13. A. Bakun, in *The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change*, D. Pauly and I. Tsukayama, Eds. (International Center for Living Aquatic Resources Management, Manila, Philippines, 1987), pp. 46–74; A. Bakun and R. Mendelssohn, in (*14*).
14. D. Pauly, P. Muck, J. Mendo, I. Tsukayama, Eds., *The Peruvian Upwelling Ecosystem: Dynamics and Interactions* (International Center for Living Aquatic Resources Management, Manila, Philippines, in press).
15. M. Tom, in preparation.
16. W. Wooster, D. Fluharty, Eds., *El Niño North* (University of Washington Sea Grant Program, Seattle, 1985).
17. J. Picaut, *Calif. Coop. Oceanic Fish. Inves. Rep.* **26**, 41 (1985).
18. L. Legendre and S. Demers, *Can. J. Fish. Aquat. Sci.* **41**, 2 (1984).
19. A. Bakun, in *L'Homme et les Ecosystems Halieutiques*, J. P. Troadec, Ed. (Institut Français de Recherche pour l'Exploitation de la Mer, Paris, 1990), pp. 155–187.
20. P. Cury and C. Roy, *Can. J. Fish. Aquat. Sci.* **46**, 670 (1989).
21. F. P. Chavez, R. T. Barber, M. P. Sanderson, in (*14*).
22. R. Lasker, in *Toward a Theory of Biological-Physical Interaction in the World Ocean*, B. J. Rothschild, Ed. (Kluwer, Dordrecht, 1989), pp. 173–182.
23. G. A. Jackson *et al.*, *Eos* **70**, 146 (1989); M. S. Quimby-Hunt, P. Wilde, W. N. E. Berry, paper presented at the First Workshop on Global Climate Change and Its Effects on California, University of California, Davis, 10 to 12 July, 1989.
24. On the other hand, the trade winds in the tropical Pacific likewise seem to have increased during this same period [K. D. B. Whysall, N. S. Cooper, G. R. Bigg, *Nature* **327**, 216 (1987)]. Whether seasonally increased alongshore winds along the continental boundaries (equatorward along the eastern ocean boundary, poleward along the western boundary) resulting from enhanced onshore-offshore temperature contrasts could contribute to an increased trade wind circulation is a matter for further study.
25. Indicated significance levels are taken directly from standard tables of the Student's *t* distribution, without adjustment for residual autocorrelation.

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Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*)

Andrew Bakun and Richard H. Parrish

Bakun, Andrew, and Parrish, Richard H. 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). – J. Cons. int. Explor. Mer, 46: 269–283.

We extend a framework of comparative climatology of reproductive habitats of neritic pelagic fishes, heretofore focused on temperate eastern ocean upwelling systems, by adding a tropical western ocean example. Maritime weather reports off southeastern Brazil are summarized to yield distributions of wind stress, Ekman transport, wind mixing index, insolation, cloud cover and sea surface temperature for two-month segments of the seasonal cycle. These are used to describe seasonal aspects of the oceanography of the region. Vigorous coastal upwelling occurs in the vicinity of Cabo Frio–Cabo São Tomé through most of the year, relaxing only during austral fall. Directly downstream of this upwelling center lies the coastal bight between Cabo Frio and Cabo Santa Marta Grande, within which offshore Ekman transport and wind-induced turbulent mixing fall to coastwise minima. The near-coastal water column within the bight, while vertically homogeneous during winter, becomes stably stratified during summer. We infer a rather enclosed circulation pattern within the bight, with the main Brazil Current flow skirting across the bight opening rather than following the coastline into the bight interior. This coastal bight constitutes the primary reproductive habitat of the Brazilian sardine. Peak spawning activity during summer serves to place larvae into a stable, enriched environment, where they enjoy high likelihood of retention. In the manner of achieving these advantages, the reproductive strategy of this population appears to be a nearly exact analogue to those of sardine populations inhabiting eastern boundary current upwelling systems, in spite of its western ocean boundary location and the fact that a warmer water genus is involved. The conclusion is that this *Sardinella* population is solving similar dominant environmental problems to those faced by the more temperate *Sardinops* and *Sardina* stocks of eastern boundary systems, only at a warmer temperature range. These findings lend support to the idea that our various fragments of experience of environmental effects on fish populations are not unconnected anecdotes, as they are often treated, but are amenable to scientific generalization.

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Introduction

Recruitment variability in fish populations remains the key unsolved problem of fishery science, even after many decades of committed scientific effort. The problem has been extremely difficult to address at the population level via the experimental approach. And the empirical approach, whereby correlations are sought between recruitment time series and time series of environmental variables, has yielded only limited insights (Bakun, 1984; Shepherd *et al.*, 1984).

Because the detailed causal mechanisms are largely unknown, there is presently no way effectively to cope with large-amplitude quasi-random recruitment variability, occurring on the year-to-year time scale, which largely obscures the essential signals needed to foresee the effects of fishery exploitation over longer time scales. These signals include the functional form of the relationship between stock size and expected recruitment, trends in stock productivity, interspecies interactions, effects of climatic variability or habitat alteration, etc. Lacking the ability to resolve these signals, the methodologies of fishery science must rely on arbitrary assumptions concerning the crucial factors involved in projections of the viability of an industry or in the preservation of a resource over multi-year time periods. The oversimplification and non-realism of these controlling assumptions has in many cases resulted in failure of the scientific methodologies, often with severe socio-economic consequences (Glantz, 1984).

Fishery-based data series tend to be too short, and the variability too non-random, for objective filtering techniques to be effective in detecting and allowing for this inter-year noise. Therefore, an improved degree of insight into the actual mechanisms controlling the variability appears to be required in order to identify the underlying signal. As one approach for developing the needed level of insight, Bakun and Parrish (1980) suggested use of interregional comparative studies. Mayr (1982) calls the experimental method and the comparative method "the two great methods of science", and cites the comparative method as being particularly appropriate to situations not amenable to experimental controls; for example, it has been the basis for "nearly all of the revolutionary advances in evolutionary biology".

Parrish et al. (1983) assembled seasonal distributions of ocean surface processes in the California, Peru, Canary, and Benguela Current regions and identified a pattern of simultaneous avoidance of strong offshore-directed transport and of wind-induced turbulent mixing in the spawning habits of the anchovies and sardines inhabiting those temperate eastern ocean boundary upwelling systems. The existence of a consistent inter-regional pattern suggests that these particular factors may well have exerted major controls on reproductive success during the period over which the observed seasonal and geographical spawning adaptations were developed. Bakun (1985) further elaborated the rationale for using comparative studies of the oceanography of preferred spawning habitats both to identify the environmental factors controlling reproductive success and to build confidence (or detect spuriousness) in empirical findings.

In looking for additional examples which might serve as useful comparative analogs to the temperate eastern boundary pelagic fish stocks, we are faced with two major alternatives: (1) to shift attention to stocks of similar species which inhabit the dynamically quite different western boundary current regions, or (2) to redirect our focus toward closely related tropical genera, such as *Sardinella*, which could be employing similar life cycle strategies, but at a warmer temperature range.

In this study, we take both steps at once and address the western boundary current *Sardinella* population located off the southeastern coast of Brazil (Fig. 1). The Brazil Current is a representative poleward-flowing western boundary current, albeit a less intense flow than the Kuroshio or the Gulf Stream (Stommel, 1966). Olson *et al.* (1988) find the mean latitude of separation of the Brazil Current from the shelf break to be 35.8 ± 1.1°; thus over essentially the entire latitude range addressed in the study, the area to seaward of the 1000 m isobath is dominated by southward or southwestward Brazil Current flow (Fig. 1).

The Brazilian sardine (*Sardinella braziliensis* = *Sardinella aurita*) represents a warmer water counterpart

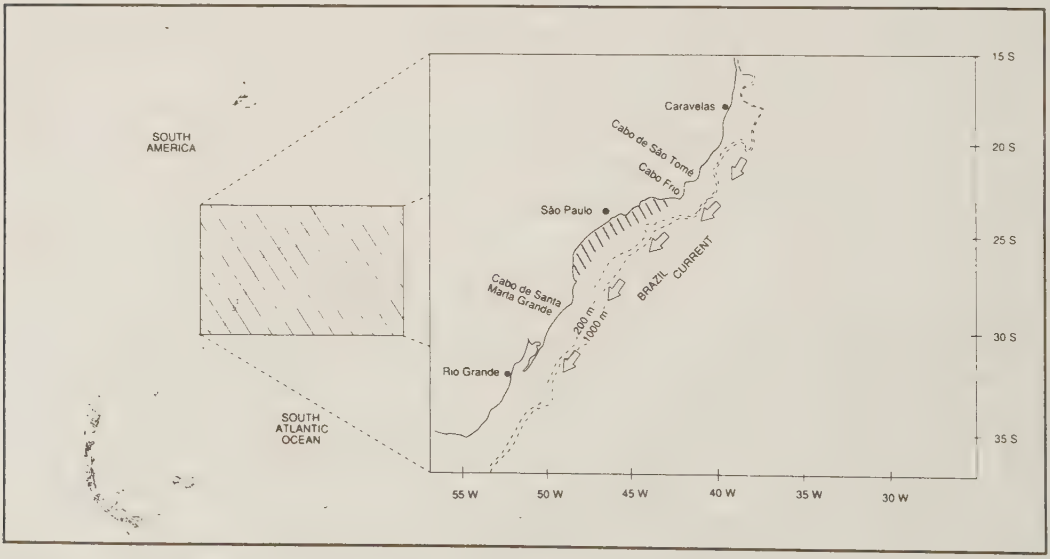


Figure 1. Study region. The area of the Brazilian sardine fishery is indicated in light shading (after Saccardo, 1983). The main spawning grounds (Bakun, MS) are located within the area indicated by diagonal hatching. The large-sçale flow of the Brazil Current generally extends shoreward to the continental shelf break (see text), as indicated by the arrow symbols.

to the sardine species of the genera *Sardinops* and *Sardina*, which have constituted very large populations in coastal upwelling regions along the eastern boundaries of the world's oceans and in the western ocean boundary region near Japan (Parrish *et al.*, 1989). *Sardinella* is rather widely distributed on both sides of the Atlantic as well as in the Indo-Pacific and is one of the dominant genera in terms of total world fishery landings. The recent history of the Brazilian population recalls the scenario which has become familiar in the case of the exploited sardine stocks of eastern boundary currents, with landings growing rapidly to a peak (228 000T in 1973) and falling off to a lower level thereafter (Saccardo, 1983). Most recently, landings have fallen off precipitously and there is concern about the possibility of a population collapse (Y. Matsuura, pers. comm.; S. Saccardo, pers. comm.).

The seasonal distributions of environmental processes and properties presented herein are based on summaries of the historical record of marine weather reports. By international convention, such weather observations are recorded routinely by a variety of types of ships operating at sea. Observations of wind speed and direction, sea and air temperature, barometric pressure, humidity, and cloud cover included in these reports provide a basis for estimating a number of environmental variables pertinent to the study of ocean variability. The observations are made and collected, albeit at varying densities, in all regions of the world ocean in which maritime commerce takes place. All of the actual measurements are made at or above the sea surface; however, ocean variability is forced primarily at the air–sea interface and data such as these therefore provide a basis for drawing inferences about processes and conditions within the interior of the ocean environment. Thus, if effective comparative frameworks can be deduced from surface maritime data, the habitat of virtually every important exploited fish population in the world would be a potential candidate for comparative study.

In this paper we summarize the historical record of these reports available for the area off southeastern Brazil to construct seasonal distributions of (1) stress of the wind on the sea surface, (2) associated surface Ekman transport, (3) an index of wind-derived mechanical energy available for mixing of the water column, (4) rate of absorption of solar radiation through the sea surface, (5) average fraction of sky obscured by clouds, and (6) sea surface temperature. The first four items are primary forcing agents of seasonal variability in local oceanographic processes. The last two items, particularly sea surface temperature, provide some evidence of the nature and consequences of the indicated seasonal forcing.

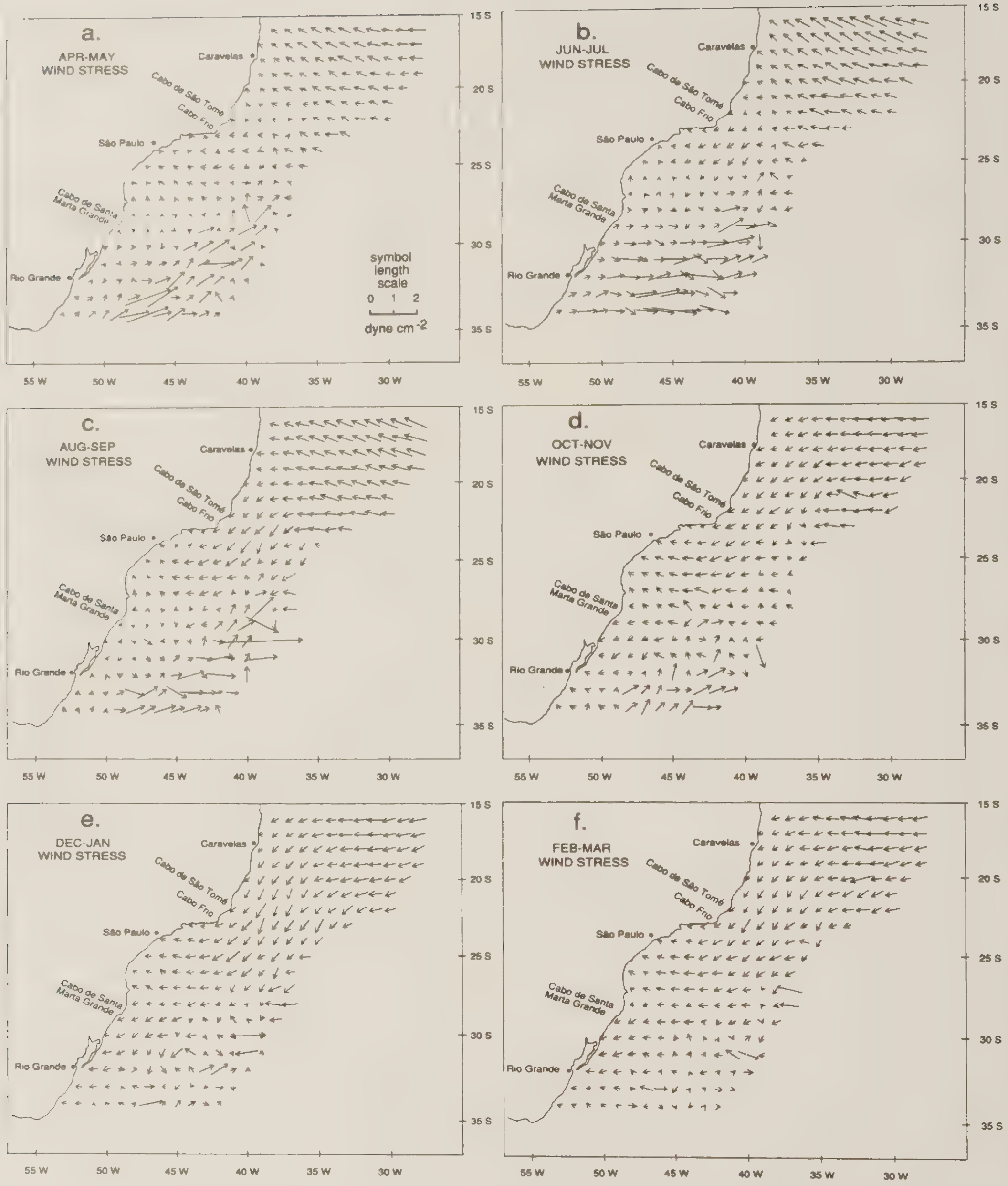
Besides being the habitat of the Brazilian sardine, historically Brazil's largest fishery stock, the study area has considerable oceanographic, ecological, and social-economic importance. The adjacent coast is the site of the great urban and industrial centers of Brazil. The local ocean ecosystem is thus potentially subject to particular stress from the impacts of human activities. Thus in addition to supporting comparative evaluation of pelagic fish reproductive strategies, the distributions presented herein may serve as inputs to a variety of marine-oriented scientific studies in the region.

Methods

Maritime reports contained in the US National Climatic Center's file of surface marine observations (Tape Data Family – 11; incorporating data from late 1800s through 1979) were grouped by one-degree latitude/longitude areal quadrangles and by two-month segments of the calendar year. Estimates of the various quantities of interest were produced from each individual report. The average value of all the estimates in each of these groups of reports was taken as the expected value for the location and two-month seasonal segment. The vector quantities, wind stress, and Ekman transport, were averaged by component (vector averaged). The one-degree quadrangles selected for these summaries are centered at intersections of a grid of even whole degrees of latitude and longitude, spanning the interval from 18°S lat to 34°S lat and extending twelve degrees of longitude offshore of the coastal boundary. Editing of the data consisted only of a gross error check to ensure physically possible values. Wind speeds greater than $50\,\mathrm{m\,s^{-1}}$ (~100 knots) were discarded.

The vector quantities (Figs. 2, 3) are displayed as discrete vector symbols, each value being derived from a data set that is independent of all other one-degree quadrangles and two-month seasonal segments. Particularly large standard errors were found to be typical of the estimates in the southern offshore portions of the gridded area, reflecting not only very low available data density in that part of the region but also highly energetic variability in actual conditions. The low degree of coherence among spatially-adjacent values visible in that area of Figures 2 and 3 should thus be regarded as largely reflecting lack of stability of the estimates rather than as indicating real small-scale spatial differences in characteristic value.

In preparing the contoured maps of the scalar quantities (Figs. 4, 5, 6), some minimal spatial smoothing has been applied. A three by three grid point version of the median smoother (Tukey, 1977) was employed to deal with the intense "bull's-eyes" that largely obscured the underlying significant pattern in the more data-poor offshore areas. However, in cases where this procedure may have removed features which were similarly indicated by directly-adjacent independent samples and which were judged to be real after examination of the standard errors of the individual sample means, the contours were subjectively adjusted to re-insert the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APR-MAY
WIND STRESS
b.
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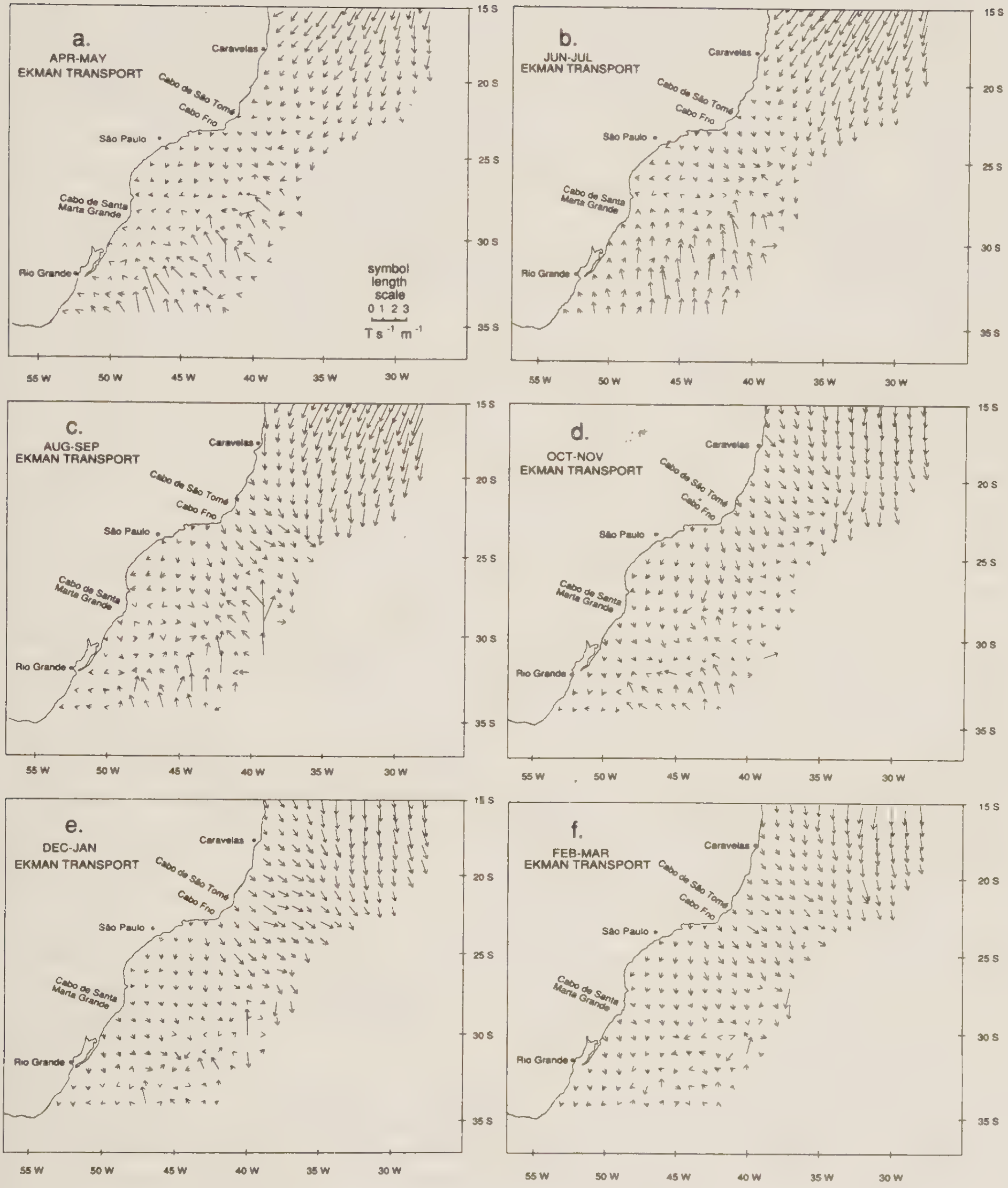
WIND STRESS
c.
AUG-SEP
WIND STRESS
d.
OCT-NOV
WIND STRESS
e.
DEC-JAN
WIND STRESS
f.
FEB-MAR
WIND STRESS
Caravelas
Cabo de São Tomé
Cabo Frio
São Paulo
Cabo de Santa Marta Grande
Rio Grande
symbol length scale
0 1 2
dyne cm -2
15 S
20 S
25 S
30 S
35 S
55 W
50 W
45 W
40 W
35 W
30 W

Figure 2. Sea surface wind stress distributions for two-month segments of the seasonal cycle. Stress is proportional to vector symbol length. A symbol length scale is provided; units are dyne cm^{-2} (10^{-1} pa). (a) Aprii–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.


a.
APR-MAY
EKMAN TRANSPORT
b.
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EKMAN TRANSPORT
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AUG-SEP
EKMAN TRANSPORT
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OCT-NOV
EKMAN TRANSPORT
e.
DEC-JAN
EKMAN TRANSPORT
f.
FEB-MAR
EKMAN TRANSPORT
Caravelas
Cabo de São Tomé
Cabo Frio
São Paulo
Cabo de Santa Marta Grande
Rio Grande
symbol length scale
0 1 2 3
T s^-1 m^-1
15 S
20 S
25 S
30 S
35 S
55 W
50 W
45 W
40 W
35 W
30 W

Figure 3. Surface Ekman transport distributions for two-month segments of the seasonal cycle. Transport is proportional to vector symbol length. A symbol length scale is provided; units are metric t s^{-1} across each meter width. (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

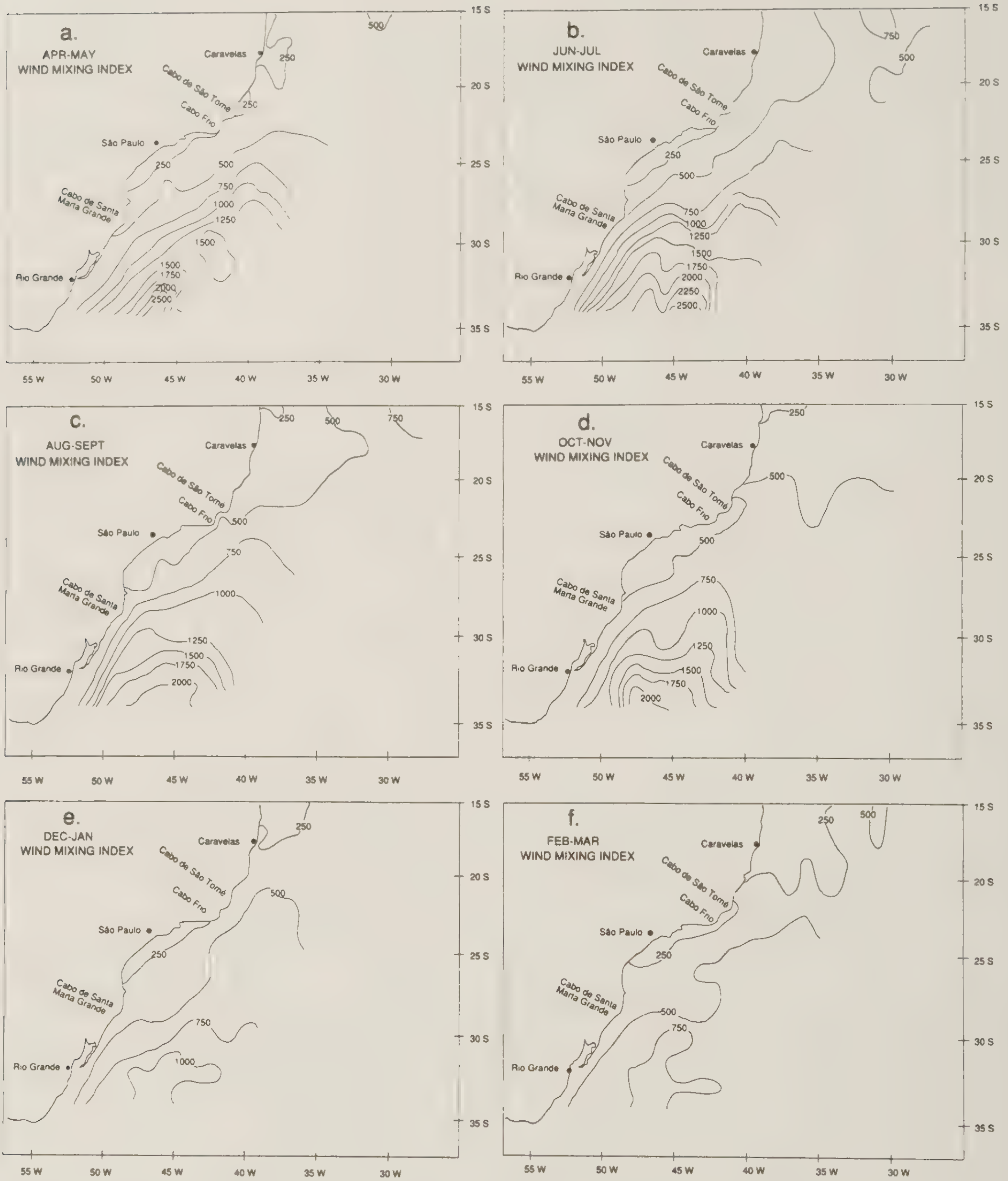

a.
APR-MAY
WIND MIXING INDEX
b.
JUN-JUL
WIND MIXING INDEX
c.
AUG-SEPT
WIND MIXING INDEX
d.
OCT-NOV
WIND MIXING INDEX
e.
DEC-JAN
WIND MIXING INDEX
f.
FEB-MAR
WIND MIXING INDEX
Caravelas
Cabo de São Tomé
Cabo Frio
São Paulo
Cabo de Santa Marta Grande
Rio Grande
250
500
750
1000
1250
1500
1750
2000
2250
2500
15 S
20 S
25 S
30 S
35 S
55 W
50 W
45 W
40 W
35 W
30 W

Figure 4. "Wind cubed" index of rate of addition to the ocean, by the wind, of mechanical energy available for turbulent mixing of the upper water column; nominal units are $m^{-3} s^{-3}$. (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

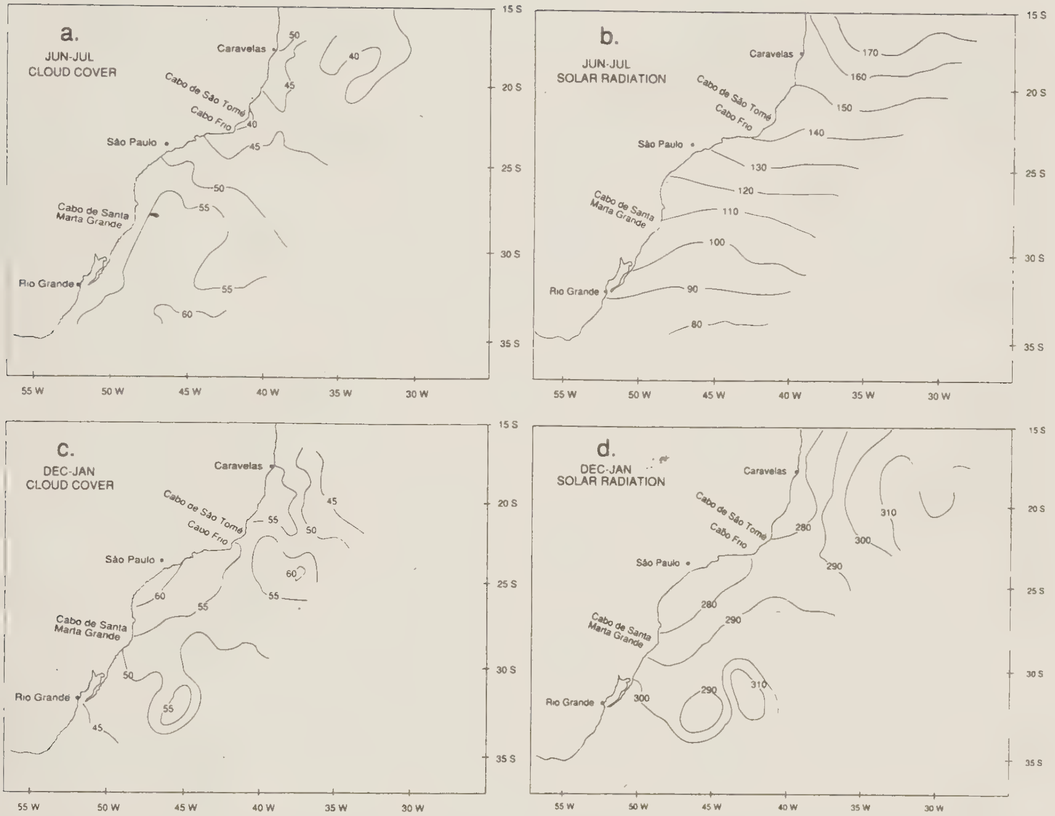

a.
JUN-JUL
CLOUD COVER
b.
JUN-JUL
SOLAR RADIATION
c.
DEC-JAN
CLOUD COVER
d.
DEC-JAN
SOLAR RADIATION
Caravelas
Cabo de São Tomé
Cabo Frio
São Paulo
Cabo de Santa Marta Grande
Rio Grande
15 S
20 S
25 S
30 S
35 S
55 W
50 W
45 W
40 W
35 W
30 W

Figure 5. Mean cloud cover and solar radiation. (a) Cloud cover during June–July (austral winter); (b) solar radiation absorbed through the sea surface during June–July; (c) cloud cover during December–January (austral summer); (d) solar radiation absorbed through the sea surface during December–January. Units for cloud cover distributions are percent of sky obscured. Units for solar radiation distributions are watts m^{-2} (to convert to cal cm^{-2} day^{-1}, multiply values by the factor 2.064).

features. The intention has been to avoid showing features that are determined by only a single estimate (i.e. shown only in one of the two-month, one-degree lat/long sample means).

Wind stress

In estimating the stress of the wind on the sea surface we use the same procedure as established by Bakun *et al.* (1974). An estimate of the stress is formed from each wind report according to the standard formulation

$$\vec{\tau} = \rho C_D |\vec{v}| \vec{v} \tag{1}$$

where $\vec{\tau}$ represents the stress vector, ρ is the density of air (considered constant at 0.00122 gm cm^{-3}), C_D is an empirical drag coefficient (considered constant at 0.0013), $|\vec{v}|$ is the scalar wind speed, and $\vec{v}$ is the vector wind velocity. Reports where the wind direction is coded as "variable" are incorporated as calms (zero wind speed) in the stress summaries (see discussion by Bakun (1987)).

Ekman transport

On the seasonal time scales being addressed, the drift of waters at the sea surface under the direct action of the wind stress is satisfactorily characterized by the simplified idealization known as Ekman transport (Ekman, 1905). The net Ekman transport, $\vec{E}$, integrated over the layer of some several tens of meters beneath the sea surface in which it occurs, is given by

$$\vec{E} = \vec{k} \times \frac{\vec{\tau}}{f} \tag{2}$$

where $\vec{k}$ is a unit vector directed vertically upward, "×"

denotes the vector ("cross") product, $\vec{\tau}$ is the wind stress vector and f is the Coriolis parameter ($f = 2\omega \sin \phi$) where ω is the angular velocity of the earth's rotation and ϕ is the latitude (negative degrees in the southern hemisphere). Net Ekman transport is thus directed perpendicularly to the left of the wind stress in the southern hemisphere.

Wind mixing index

The rate at which the wind imparts mechanical energy to the ocean to produce turbulent mixing of the upper water column is roughly proportional to the third power, or "cube", of the wind speed (Elsberry and Garwood, 1978). A "wind mixing index", which is simply the mean of the cube of the observed wind speeds in each of the seasonal/areal samples, provides a guide to the variability in this particular process (Bakun and Parrish, 1982). In this case wind reports with the direction coded as "variable" are handled differently than in the stress summaries. Here the wind speed enters as a scalar quantity and directionality is immaterial, and so the wind speed value is incorporated directly as coded in the report.

Solar radiation

Net incoming solar radiation Q_s, absorbed by the ocean was estimated from each individual report according to Bakun's (1987) adaptation of Nelson and Husby's (1983) computational procedure. The procedure is based on the standard formation

$$Q_s = (1 - \alpha)Q_0(1 - 0.62C + 0.0019h) \qquad (3)$$

where α is the fraction of incoming radiation reflected from the sea surface, Q_0 is the sum of the direct and diffuse radiation reaching the ground under a cloudless sky, C is the observed total cloud amount in tenths of sky covered, and h is the noon solar altitude. Q_0 is estimated according to the procedures and tables presented by List (1949), using a four-by-four element curvilinear interpolation of the table entries via Bessel's central difference formula and assuming the atmospheric transmission coefficient of 0.7 recommended by Seckel and Beaudry (1973). The linear cloud correction in Equation (3) is as suggested by Reed (1977); Reed's recommendation that no correction be made for cloud amounts less than 0.25 of total sky was followed. Sea surface albedo, α, was extracted from Payne's (1972) tables, following Nelson and Husby's (1983) algorithm which involves entering the tables with the 0.7 atmospheric transmission coefficient, reduced by a factor equal to the cloud correction applied in Equation (3), and with the mean daily solar altitude.

Results

Wind stress

The area of study lies generally between, but definitely under the influence of, the strong steady easterly trade wind circulation which dominates the tropical region to the north and the violently variable westerlies of the "roaring forties" to the south. The degree of influence of these respective systems varies seasonally, particularly so in the case of the westerlies, with the pattern shifting somewhat northward in austral winter (Jun–Sep) and shifting back southward in austral summer (Dec–Mar).

Thus during austral autumn (Fig. 2a) the wind stress in the northern portion of the gridded area is directed toward the coast in conformity with the trade wind circulation which flows in the same direction. In the southern portion, the northward extension of the zone of strong erratic westerlies (eastward stress) is evident. Off Cabo Frio and Cabo São Tomé, the mean stress is weak and directed toward the coast.

As the season progresses, the region of strong easterly (westward) stress expands southward. By late winter (Fig. 2c) strong westward stress is evident in the offshore half of the gridded area as far south as 24°S lat. Nearer the coast, the wind stress is directed generally alongshore toward the southwest, forming an alongshore maximum off Cabo Frio and Cabo São Tomé, parallel to the Brazil Current flow which is indicated in Defant's (1961) charts to be particularly strong at that season of the year. Substantial westerly (eastward) stress extends during this season to well north of 30°S lat (in the offshore portion of the gridded area). Near the coast south of Cabo Santa Marta Grande, the net resultant stress falls to generally low values.

By early summer (Fig. 2e) the stress near the coast is alongshore and poleward for nearly the entire length of the area studied, and by late summer (Fig. 2f) the effect of the westerlies has essentially vanished from the gridded area. However, the alongshore stress of Cabo Frio and Cabo São Tomé remains substantial until its relaxation in late fall.

Throughout the year, the area near the shore within the coastal bight lying between Cabo Frio and Cabo Santa Marta Grande is an area of minimal net average stress. The offshore increase in stress results in a general pattern of cyclonic (clockwise in the southern hemisphere) horizontal shear in the stress pattern. Also there is a general cyclonic curvature to the pattern. The shear and curvature combine to constitute a predominance of cyclonic wind stress curl in the area. In our studies of similar coastal bights in eastern boundary current regions (Bakun, MS), such a predominance of cyclonic wind stress curl has invariably been reflected in a rather enclosed cyclonic gyral circulation. The existence of the poleward flowing Brazil Current seaward of the bight area would tend to reinforce the tendency in this case. Matsuura (1986) and Castro Filho *et al.* (1987) present sample vertical sections which show areas of doming of subsurface structure shoreward of the continental shelf break, suggesting a degree of baroclinically-compensated cyclonic gyral geostrophic flow pattern within the bight.

Ekman transport

The seasonal distributions of Ekman transport corresponding to the wind stress distributions (Fig. 2) are presented in Figure 3. The seasonal cycle of course directly follows the seasonal cycle of wind stress. Of major interest is the offshore-directed Ekman transport in the vicinity of Cabo Frio and Cabo São Tomé, which is relaxed in the austral autumn (Fig. 3a) but intensifies through the early winter (Fig. 3b) to reach a maximum in the late winter and early spring (Fig. 3c, d) which is maintained essentially through the entire austral summer (Fig. 3e, f). This pattern of seasonal offshore Ekman transport is remarkably similar to the patterns which drive the classical seasonal coastal upwellings of the eastern boundary regions (Wooster and Sievers, 1970; Bakun *et al.*, 1974; Wooster *et al.*, 1976; Parrish *et al.*, 1983). Note also that the magnitude of offshore transport continues to increase with distance from the coast, out to more than 200 km from shore (a consequence of the cyclonic wind stress curl cited in the previous section). Thus the coastal upwelling that occurs within several tens of kilometers of the coast will be augmented by additional upward "Ekman pumping" driven by the general divergence of Ekman transport further offshore.

Within the coastal bight south of Cabo Frio there is a local minimum in the general offshore-directed Ekman transport that extends over most of the region during spring and summer (Fig. 3d, e, f).

Wind mixing index

As regards the generation of turbulent energy available for mixing the water column, the effect of the erratically-varying westerlies impinging from the south dramatically outweighs the steadier trade wind circulation affecting the northern portion of the gridded area. The seasonal differences are very large in the southern offshore portion most affected by the westerlies, with the effects being extreme in austral winter (Figs. 4b, c) when wind mixing index values of several thousand $m^3 s^{-3}$ occupy a substantial area, and most relaxed in late summer (Fig. 4f).

In contrast, the coastal bight from Cabo Frio to Cabo Santa Marta Grande appears as an area of very gentle wind-induced turbulent mixing, with average wind mixing index values tending to be less than $250 m^3 s^{-3}$ except during late winter and early spring when the values tend to be slightly greater (Fig. 4c, d). By early summer, wind effects within the bight diminish such that the area enclosed by the $250 m^3 s^{-3}$ contour covers essentially the entire bight area (Fig. 4e). Castro Filho *et al.* (1987) report little stratification over the inner shelf during winter; however, during summer a two-layer vertical stratification builds up, with a strong thermocline at mid-depths. With the relaxation of coastal upwelling in late summer, even the Cabo Frio–Cabo São Tomé upwelling center falls within the $250 m^3 s^{-3}$ contour (Fig. 4a).

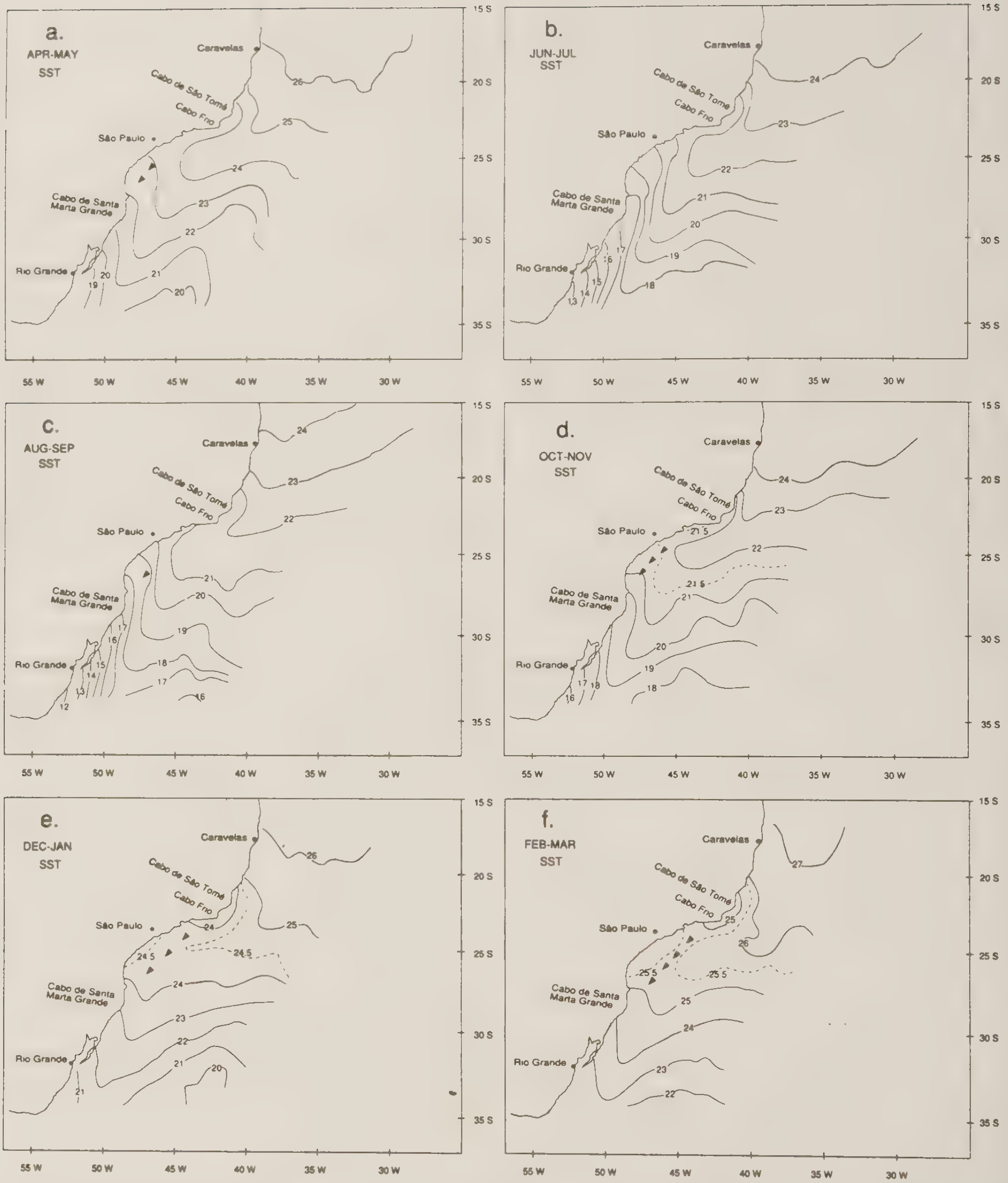
Solar radiation and cloud cover

During the austral winter the cloud cover (Fig. 5a) varies from less than 40% of sky obscured on average in some offshore locations at the northern edge of the study area, to greater than 60% at some locations at the southern edge. The upwelling center off Cabo Frio and Cabo São Tomé is marked by a local minimum of cloud cover along the coast, as is the general pattern for upwelling centers in eastern ocean boundary areas (Parrish *et al.*, 1983). The corresponding distribution of solar radiation absorbed (Q_s) during winter (Fig. 5b) shows a strong meridional gradation related to the latitudinally-varying solar angle. The effect of the cloud cover distribution is seen only in deflections of the isopleths from a strictly zonal orientation.

During the austral summer the distribution of cloud cover (Fig. 5c) continues to have a coastwise minimum in the vicinity of Cabo Frio and Cabo São Tomé. The coastal bight immediately to the south contains a relative maximum in cloud cover. At this season the noon position of the sun is nearly directly overhead and the shape of the Q_s isopleths (Fig. 5d) is strongly influenced by the cloud cover distribution. The Cabo Frio–Cabo São Tomé upwelling center represents a local coastwise maximum in solar radiation absorbed. The summer values of Q_s (Fig. 5d), representing energy available for (1) absorption by water molecules, thereby warming the ocean surface layer, or (2) absorption by plant pigments to provide the energy for photosynthetic production of organic matter, tend to be more than twice the winter values (Fig. 5b) both at the upwelling center and within the coastal bight immediately to the south.

Sea surface temperature

Comparison of the sea surface temperature distributions (Fig. 6) with the solar radiation distributions (Fig. 5) shows little correspondence in pattern, except for the global-scale latitudinal gradations in these properties which characterize the oceans as a whole. The other ocean-atmosphere heat exchange components, i.e. long wave back radiation and evaporative and conductive heat fluxes, tend to be small compared to the short wave solar radiation input in such near-tropical regions (e.g.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27

Figure 6. Sea surface temperature distributions for two-month segments of the seasonal cycle. Units are degrees Celsius. (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March. Triangular symbols indicate locations of local one-degree lat/long average temperature minimum values occurring offshore, downstream of the Cabo Frio–Cabo São Tomé upwelling center.

Bakun, 1987); also, the long wave back radiation would have a similar pattern to the cloud cover (Fig. 5). Thus features in the sea surface temperature pattern which deviate from the global-scale pattern of zonal isotherms can apparently be ascribed to such dynamic processes as advection, upwelling, and surface cooling due to vertical mixing, rather than to local variations in sea surface heat exchange.

Evidence of the southwestward flow of the Brazil Current, parallel to the large-scale coastline trend, is seen in the strong curvature of the surface isotherms (Fig. 6) into definite tongue-like forms which extend towards the southwest, with axes generally centered some two to three hundred kilometers offshore.

Near the Cabo Frio–Cabo São Tomé upwelling center, relative cooling of the sea surface resulting from the local coastal upwelling is evident. During the fall season of quite relaxed offshore Ekman transport (Fig. 3a), the effect is seen merely as an exaggeration of the tongue-like feature (Fig. 6a). However, by early summer (Fig. 6e) the upwelling core is surrounded by closed isotherms which intersect the coast both to the north and to the south, strikingly similar in form to the closed isotherm distributions seen in similar maritime data summaries for such "classical" eastern boundary upwelling centers as Cape Mendocino in the California Current, San Juan in the Peru Current, Cap Blanc in the Canary Current, and Lüderitz and Cape Frio in the Benguela Current (Parrish *et al.*, 1983).

However, the coastal sea surface temperature anomaly (i.e. the difference between the temperature near the coast and the characteristic large-scale offshore temperature at the same latitude) characterizing this particular upwelling center is somewhat less, being of the order of 2°C rather than the 4–6° typical of the most intense eastern boundary upwelling centers. A lesser coastal temperature anomaly is not unexpected, as the offshore Ekman transport which drives the upwelling process is of considerably less strength (Fig. 7) than typically found in the eastern boundary upwelling centers. Also, the alongshore extent of the region of relatively strong upwelling is much less than in the major eastern ocean boundary systems. On the other hand, the strong turbulent mixing that characterizes the offshore area (Fig. 4) relative to the near-coastal area is different from the situation in the eastern boundary upwelling centers, where there tends to be less offshore gradient in wind mixing index values (Parrish *et al.*, 1983); this may work to lessen the relative coastal cooling seen in the sea surface temperature distribution off Cabo Frio–Cabo São Tomé.

It is interesting to note that although appreciable offshore-directed Ekman transport exists well to the north of Cabo São Tomé (to at least 18°S lat) from late winter through the entire summer (Fig. 3c, d, e, f), the marked coastal cooling typical of an upwelling center is not highly evident in the sea surface temperature distributions north of about 20°S lat (Fig. 6), except

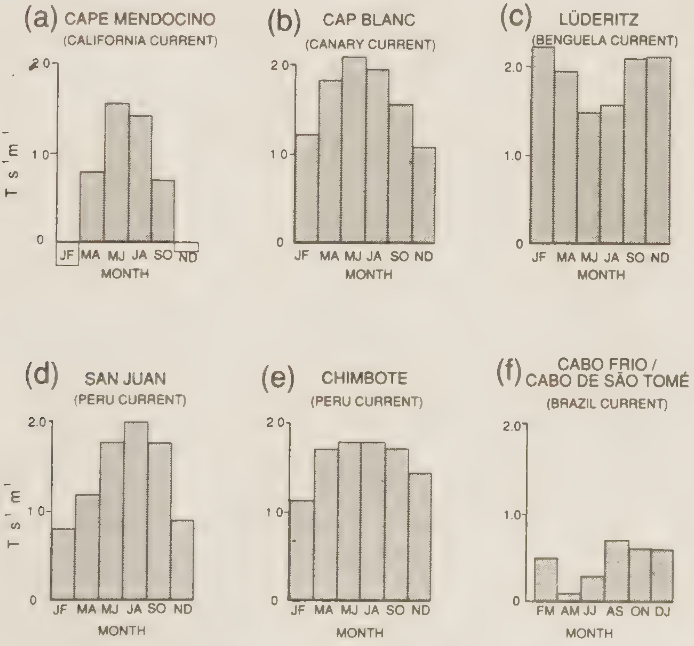

Figure 7. Offshore component of Ekman transport in major coastal upwelling centers by two-month segments of the seasonal cycles. Units are metric t s^{-1} across each meter width. (a) Cape Mendocino, California; (b) Cap Blanc, Mauritania; (c) Lüderitz, Namibia; (d) San Juan, Peru; (e) Chimbote, Peru; (f) Cabo Frio, Brazil.

perhaps in late summer (Fig. 6f). Since coastally-trapped propagation (e.g. Gill and Clarke, 1974) is directed equatorward along western ocean boundaries, the hypothesis that the offshore transport may be replenished by alongshore flow from the upwelling center to the south appears to be untenable since that would imply southward propagation of the forcing signal. Certainly, there are other hypothetical explanations available. For example, friction associated with Brazil Current flow impinging against the Abrolhos Bank (which can be seen in Figure 1 in the major seaward bulge of the isobaths to the east and south of Caravelas) may lead to the flow becoming locally sub-geostrophic, resulting in cross-isobar (shoreward) surface transport which could offset the offshore Ekman transport. However, in this case surface data alone cannot provide a definitive explanation.

A cool core extends to the southwest of the upwelling center across the opening of the coastal bight between Cabo Frio and Cabo Santa Marta Grande. (This is indicated in Fig. 6 by triangular symbols marking the location of the minimum temperature value along each zonally-oriented line of one degree lat/long areal summaries, in cases where the minimum is not at the coast.) This offshore cool core appears to be an advective feature, suggesting that the main current flow must be directly across the open outer edge of the bight rather than following the curvature of the shoreline into the interior of the bight. Warmer surface water exists along the coast shoreward of this cool core, strengthening the impression of a rather enclosed cyclonic gyral circulation within the bight, which was inferred earlier from the wind stress pattern. Matsuura (1986) shows a very narrow band of less saline surface water confined directly against the coast; this would tend to raise the sea height at the coast, promoting northeastward geostrophic flow adjacent to the coast within the bight to close the gyral circulation pattern. In fact, without such a flow to provide a combination of Coriolis and centrifugal forces to balance the horizontal pressure gradient implied by the band of fresher water, it is difficult to envision dynamics that could allow the band to remain confined to the coast in the manner observed.

It is possible that the cool core denoted by the triangle symbols could also be interpreted as being at least partially due to northeastward advection of cooler coastal waters from south of the bight, particularly during the fall through spring seasons (Fig. 6a, b, c, d). The vertical sections presented by Castro Filho *et al.* (1987) are somewhat complex and do show the doming of the density structure to be largely confined to the outer half of the bight during winter. In any case it is clear that the large-scale Brazil Current flow does not sweep directly through the bight interior, but rather skirts across the seaward edge of the bight opening. Thus the interior of the bight must be characterized by one or more semi-enclosed gyral circulation patterns.

Discussion

Several hypotheses concerning environmental effects on the reproductive strategies of small coastal pelagic fishes have been the object of particular recent scientific interest among researchers working in the California Current system and in other eastern boundary current systems:

1. Lasker (1975, 1981a, 1981b) has suggested that wind-induced turbulent mixing could destroy fine-scale food particle aggregations required for successful first-feeding of newly hatched larvae; Peterman and Bradford (1987) demonstrate a time series relationship between early survival of anchovy larvae (*Engraulis mordax*) in the Southern California Bight and the frequency of periods of weak winds of sufficient duration to allow formation of aggregations of food organisms.
2. Parrish *et al.* (1981) survey the diverse reproductive habits of a wide variety of California Current fishes. They identify a common pattern of avoidance of placing pelagic eggs and larvae into circumstances where they would be rapidly transported and dispersed offshore. In particular, they point out that adult coastal pelagic fishes of that region migrate long distances between feeding and spawning grounds, with the result that spawning occurs under the favorable conditions of the Southern California Bight, where offshore Ekman transport is minimal and a closed gyral circulation pattern may serve to retain drifting larvae within the bight.
3. Parrish *et al.* (1983) show that in eastern boundary current regions large stocks of sardines and anchovies tend to spawn in coastal bights downstream (with respect to the large-scale boundary current flow) of major upwelling centers; Bakun and Parrish (1980) show a correlation, at a temporal lag appropriate to the advective transit time, between interyear variability in upwelling intensity at the major upwelling center near Cape Mendocino and interyear recruitment variability of California sardine (*Sardinops sagax*) spawning more than 500 km downstream in the Southern California Bight.

The reproductive strategy of the Brazilian sardine appears to be in close conformity with all three classes of hypotheses. The population is largely resident within the coastal bight between Cabo Frio and Cabo Santa Marta Grande, although adults may leave the bight to feed near the Cabo Frio–Cabo São Tomé upwelling center. Spawning is confined to the bight (Fig. 1) and peaks during summer, particularly during the months of December and January (Matsuura, 1979; Saccardo, 1983). Reproductive activity appears to cease entirely during fall and winter (April to September).

Spawning in the summer serves to place the larvae within an enriched environment directly downstream (with respect to Brazil Current flow) from the Cabo Frio–Cabo São Tomé upwelling center. The timing is such that this occurs during a period of continued rather vigorous upwelling, slightly lagging the seasonal upwelling peak (as appropriate to allow time for upwelling-enriched "planktonic food web" effects to be advected toward, and diffused into, the bight area to enhance the availability of minute food particles needed by the larvae). This is the season when extremely low production of turbulent mixing energy characterizes the entire interior of the coastal bight where spawning occurs (Fig. 4e). This also corresponds to the seasonal peak of solar radiation entering the ocean (Fig. 5d), when energy available for photosynthesis is at a maximum and when a strong tendency for stratification of the upper water column would tend to inhibit destruction of fine-scale structure of food particles by turbulent mixing. In addition, offshore Ekman transport relaxes to a local minimum within the coastal bight (Fig. 3e) and we have inferred a rather closed geostrophic circulation pattern which would also tend to retain larvae and oppose their offshore dispersal and loss from the coastal habitat.

The degree of similarity to the seasonal and geographical reproductive adaptations exhibited by the California sardine stock is remarkable. In addition to spawning habits, the similarity to the California stock also includes the migration of larger adults, out of the coastal bight which serves as reproductive habitat, to feed in the highly productive but more turbulent and dispersive upstream region near the upwelling center.

Thus the seasonal and locational adaptations in the spawning habits of the *sardinella* of southeastern Brazil appear to be tuned in an identical manner, to solve a very similar set of environmental problems, as are those of the sardine which spawns in the Southern California Bight. This is in spite of the very different environmental contexts (i.e. tropical versus temperate, and western boundary current versus eastern boundary current, settings) and of the fact that different genera (*Sardinella* versus *Sardinops*) are involved. Parrish *et al.* (1983) have indicated strong analogies in life-history strategy between the Southern California sardine stock and other eastern boundary current sardine stocks which choose spawning habitats within coastal bights downstream of upwelling centers. Thus the Brazilian population would also appear to be quite analogous, with respect to environmental/life-history linkages, to such other important sardine stocks as the Peru Current stock spawning in the large coastal bight centered near Africa, Chile, and the Canary Current stocks spawning in coastal indentations near Casablanca, and near Sidi Ifni, Morocco.

This represents an encouraging finding in several respects. It supports the hypothesis that insights into the nature and mechanisms of recruitment variability gained from relatively well-studied coastal pelagic fish stocks, such as those of the California and Peru Current systems, may have utility for a wider variety of coastal pelagic stocks around the world. It provides support for an assumption of analogy among multiple regional systems which may aid (1) in recognizing informative patterns of biological–physical interaction and (2) in building confidence in weak empirical relationships that exhibit interregional consistency (Bakun, 1985). It also implies that process-oriented field activities addressing the mechanisms controlling recruitment variation at the population level, which tend to present substantial operational problems, may reasonably be sited in settings selected for special amenability to the particular operational design, with the expectation that results may be applicable to a number of other settings with important fishery management and industrial concerns.

The peak size of the Brazilian population has been only a fraction of that of the major eastern boundary sardine populations, which have all yielded maximum annual landings approaching or exceeding a million tons. A plausible hypothesis for the difference is the smaller magnitude of the Brazilian coastal upwelling system, both in intensity of the offshore Ekman transport of surface waters (Fig. 7f) which constitutes the local driving mechanism for the upwelling and in the size (i.e. alongshore extent) of the upwelling center. In addition, whereas in eastern boundary current situations advection is from the sub-polar regions towards the tropics, in western boundary systems such as the Brazil Current, the alongshore flow is from the tropics toward the poles; thus the water advected horizontally into the system might be expected to be less rich in dissolved nutrient salts, and also in "seed populations" of organisms adaptable to the conditions and capable of utilizing the enrichment associated with an upwelling center.

Assuming that the recent abrupt decline in catches does not portend the final, most unfortunate analogy to the case of the California sardine, i.e. total long-term population collapse, the moderate size of the Brazilian population and its relatively confined habitat located near major ports and scientific institutions may serve to make it a particularly amenable setting for population-level recruitment studies such as the "SARP"-type exercises (Anon., 1987) being promoted under the International Recruitment Programme (IREP) within the IOC–FAO Programme of Ocean Science in Relation to Living Resources (OSLR). Our conclusions tend to support the idea that a well-posed program of scientific study of even a single example such as the Brazilian sardine might produce insights that could be beneficially applied to other important stocks around the world.

Concluding remarks

In concluding this paper we should acknowledge our recognition of the "pitfalls" inherent in any over-simplistic and overoptimistic "leap" to a conclusion of analogy among diverse fish populations, biological communities, and ocean habitats. Admittedly, the results presented here are suggestive rather than conclusive. However, science generally progresses by making assumptions which lead to conceptual frameworks within which the various available data can be categorized and arrayed for examination; these frameworks are generally discarded only after they have supported progress to the extent that it becomes clear they are no longer adequate.

The recruitment question has proven to be very resistant to scientific solution when addressed, in the conventional manner, in the context of any single autonomous fish stock and habitat. Well-posed field studies at the population level are difficult and expensive. The idea that a few process-oriented experimental efforts mounted in particularly amenable population and habitat settings could support and progressively advance a broadly-based framework of comparative scientific insight has considerable attraction (Bakun, in press). The alternative of having to repeat each step, separately and in the same way, for every important fish population in the world is a daunting prospect which is far beyond the resources that are presently available for the purpose. The true situation probably lies somewhere between these alternatives. In such a case it would seem that the most economical and effective approach would be to begin to attempt to structure scientific effort on the basis of the more optimistic assumption, as long as the fact that it remains an assumption continues to be well recognized. Even if the assumption were totally in error the detriment to having employed it would be slight. However, in the much more likely event that it is correct to some substantial degree to miss the opportunities afforded would be unfortunate indeed.

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References

Anon. 1987. IOC–FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Second Session. Reports of Meetings of Experts and Equivalent Bodies SC–87/WS/41. Intergovernmental Oceanographic Commission, Unesco, Paris, 37 pp.

Bakun, A. 1984. Report of the Working Group on Environmental Studies and Monitoring. *In* Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 41–54. Ed. by G. D. Sharp and J. Csirke. FOA Fish. Rep., 291(1), 102 pp.

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep., 26: 30–40.

Bakun, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953–84. *In* The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change, pp. 46–74. Ed. by D. Pauly and I. Tsukayama. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesselschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 351 pp.

Bakun, A. Recruitment and its relationship to environment: accessible pathways to greater insight. *In* Simposio Internacional Sobre Recursos Vivos y Pesquerías en el Pacífico Sudeste. Ed. by R. Jordon S. Comisión Permanente de Pacífico Sur, Bogatá, Columbia. (In press.)

Bakun, A. (MS) Eastern ocean regional vorticity balance, poleward coastal counterflows, and control of seasonal surface flow pattern by the horizontal gradient of wind stress curl: an interregional comparative approach.

Bakun, A., McLain, D. R., and Mayo, F. V. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fish. Bull., US, 72(3): 843–844.

Bakun, A., and Parrish, R. H. 1980. Environmental inputs to fishery population models for eastern boundary current regions. *In* Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, pp. 67–104. Ed. by G. D. Sharp. Lima, Peru, 20 Apr–5 May, 1980. IOC Workshop Rep., 28: 323 pp.

Bakun, A., and Parrish, R. H. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep., 23: 99–112.

Castro Filho, B. M. de, de Miranda, L. B., and Miyao, S. Y. 1987. Condições hidrograficas na platforma continental ao largo de Ubatuba: variação sazonaiss e em média escale. Bolm Inst. Oceanogr., S. Paulo, 35(2): 135–151.

Defant, A. 1961. Physical oceanography. Pergamon Press, London.

Ekman, V. W. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys. 2(11): 1–55 (reprinted in J. Cons. Explor. Mer, 20(2), 1954).

Elsberry, R. L., and Garwood, R. W., Jr. 1978. Sea-surface temperature anomaly generation in relation to atmospheric storms. Bull. Am. Meteorol. Soc., 59: 786–789.

Gill, A. E., and Clarke, A. J. 1974. Wind-induced upwelling, coastal currents, and sea level changes. Deep-Sea Res., 21: 325–345.

Glantz, M. H. 1984. Report of the Working Group on Societal Implications of Varying Fishery Resources. *In* Reports of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 55–66. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291(1). 102 pp.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., US, 73: 453–462.

Lasker, R. 1981a. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California

Current: Contrasting years 1975 through 1978. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 375–388.

Lasker, R. 1981b. The role of a stable ocean in larval fish survival and subsequent recruitment. *In* Marine fish larvae: morphology, ecology and relation to fisheries, pp. 80–87. Ed. by R. Lasker. Univ. Washington Press, Seattle. 131 pp.

List, R. J. 1949. Smithsonian meteorological tables. 6th ed. Smithson. Misc. Collect. 114. Smithsonian Institution Press, Wash. DC. 572 pp.

Matsuura, Y. 1979. Distribution and abundance of eggs and larval of the Brazilian sardine, *Sardinella braziliensis*, during 1974–1975 and 1975–1976 seasons. Bull. Jap. Soc. Fish. Oceanogr., 34: 1–12.

Matsuura, Y. 1986. Contribuição ao estudo da estrutura oceanografica da região sudeste entra Cabo Frio (RJ) e Cabo de Santa Marta Grande (SC). Ciência e Cultura, 38: 1439–1450.

Mayr, E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Mass. 974 pp.

Nelson, C. S., and Husby, D. M. 1983. Climatology of surface heat fluxes over the California Current region. US Dep. Commer. NOAA Tech. Rep. NMFS SSRF-763. 155 pp.

Olson, D. B., Podestá, G. P., Evans, R. H., and Brown, O. B. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. Deep-Sea Res., 35: 1971–1990.

Parrish, R. H., Bakun, A., Husby, D. M., and Nelson, C. S. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 731–778. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Parrish, R. H., Nelson, C. S., and Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1(2): 175–203.

Parrish, R. H., Serra, R., and Grant, W. S. 1989. The monotypic sardines *Sardina* and *Sardinops:* their taxonomy, distribution, stock structure and zoogeography. Can. J. Fish. Aquat. Sci., 46(11): 2019–2036.

Payne, R. E. 1972. Albedo of the sea surface. J. Atmos. Sci., 29: 959–970.

Peterman, R. M., and Bradford, M. J. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science, 235: 354–356.

Reed, R. K., 1977. On estimating insolation over the ocean. J. Phys. Oceanogr., 7: 482–485.

Saccardo, S. A. 1983. Biología y disponibilidad de sardina (*Sardinella braziliensis*, Steindachneer, 1879) en la costa sudeste del Brasil. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, pp. 449–464. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Seckel, G. R., and Beaudry, F. H. 1973. The radiation from sun and sky over the North Pacific Ocean. (Abstr. O33.) EOS, Trans. Am. Geophys. Un., 54: 1114.

Shepherd, J. G., Pope, J. G., and Cousens, R. D. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 185: 255–267.

Stommel, H. 1966. The Gulf Stream (Second Edition). Univ. California Press, Berkeley and Los Angeles; Cambridge Univ. Press, London. 248 pp.

Tukey, J. W. 1977. Exploratory data analysis. Addison-Wesley, Reading, Mass. 506 pp.

Wooster, W. S., Bakun, A., and McLain, D. R. 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. J. Mar. Res., 34(2): 131–141.

Wooster, W. S., and Sievers, H. A. 1970. Seasonal variations of temperature, drift, and heat exchange in surface waters off the west coast of South America. Limnol. Oceanogr., 15: 595–605.

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A Birth-Interval Model for Estimating Cetacean Reproductive Rates from Resighting Data

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ABSTRACT

Three approaches are examined for estimating reproductive rates from data on multiple resighting of distinctly marked animals. The three approaches correspond to parameter estimation for three population growth models. Two of the approaches, parameter estimation for the Leslie matrix and geometric series models, are based only on known-aged individuals. A third approach, the birth-interval model, is developed making fuller use of available information. The birth-interval approach uses only known-aged individuals to estimate the first-birth ogive and uses all females with previous births to estimate the probabilities associated with various birth intervals. A Monte Carlo simulation is used to examine the bias and precision of the three methods given the quantity of data that is usually available in a multiple resighting study. All three approaches appear capable of giving unbiased estimates of population growth rate. The variance associated with such estimates is greatest for the Leslie model, less for the geometric series model and least for the birth-interval model.

INTRODUCTION

The number of repeated sightings of individually-identified cetaceans continues to increase. Many examples, including both large whales and delphinids, are discussed in this volume. Some studies will soon have 20 years of continuous data including records of thousands of sightings of identified individuals from particular populations. In many cases, the presence or absence of a calf is noted when observations are made. Thus, these sighting records include potentially valuable information on cetacean reproduction. In this paper, I examine methods for calculating reproductive rates from repeated sightings of known individuals.

The more obvious approaches used to estimate reproductive rate from resighting data tend to be biased. For example, one approach is to calculate the average number of mature females that give birth in a given year. Typically, the only measure of maturity is the presence of a calf in close proximity to the female. If the first observation of a particular cow with a calf were included in calculating an average birth rate for the population, that rate would be biased upwards. If the first observation were excluded, average birth rate would be biased downwards. A second approach is to calculate an average calving interval. Typically, these estimates are also biased. Mean calving interval is affected by a downward bias because one cannot expect to observe calving intervals that terminate after the study period. Mean calving interval is affected by an upward bias because some birth events will be missed (assuming some cows are not seen every year). The intent of this paper is to develop methods for estimating reproductive rates that are robust and unbiased.

I examine three methods for estimating reproductive rates from resighting data. (For this work, resighting data is defined as records of repeated sightings of distinctly marked individuals for which the presence or absence of a calf is unambiguously noted.) The first method is based on estimating the reproductive parameters of a Leslie matrix model. The second is based on estimating parameters for a geometric series model. Both use information collected only from known-aged individuals. Because most individuals in a resighting study will not be of known age, these methods do not utilise all sources of information and might, therefore, be expected to be relatively imprecise. If parameters are correctly estimated, both are unbiased. I also present a third method which more fully utilises available information. This new approach (termed the birth-interval model) is compared to the other two approaches with respect to bias and precision.

METHODS

Reproductive rates have no clear meaning outside of the specific model to which they apply. There is no single definition of *the* reproductive rate of a population. Although one can invent statistics that are measures of reproductive output, it is difficult to judge bias or precision in the estimation of reproductive rate except in the context of a particular model. Methods for estimating reproductive parameters of three population growth models are presented below. The accurate estimation of population growth rate is the basis of measuring bias and precision. Bias and precision are evaluated using Monte Carlo simulations.

For all three models, it is assumed that mean survival rates of mature and immature individuals can be estimated from the same resighting data (Buckland, 1990).

Leslie matrix model

The Leslie matrix model is commonly used to model growth in age-structured populations. Details of the model are presented by Leslie (1945) and in most texts on population biology (e.g. Keyfitz, 1977; Pielou, 1977). In brief, the model is based on an age-structured projection matrix. When a vector of age specific population size is multiplied by this matrix, the result is the predicted vector of age-specific abundances one time unit later. Typically only females are modelled; however, because sex may not be known for the majority of individuals in a resighting study, I model males and females combined.

Table 1

Parameters used to construct the three population growth models considered here. Parameters subscripted with x or t are vectors.

Model	Parameters	Definition
Leslie Matrix	p_x	Survival rate of age-class x
	f_x	Fecundity rate of age-class x
Geometric Series	α	First sexually mature age class
	l_α	Survival from birth to age class
	p	Mean survival rate of mature age classes
	m	Mean fecundity rate of mature age classes
Birth-Interval	p_x	Survival rate of age-class x
	β_x	Fecundity rate of age-class x for females without prior births
	γ_t	Mean fecundity at t time periods after a previous birth

The non-zero elements of the Leslie matrix include age-specific survival rates (in the first sub-diagonal) and age-specific fecundity rates (in the first row) (Table 1). The survival rates represent the probability of surviving from the beginning of one age class to the beginning of the next. The fecundity rate represents the expected number of offspring produced per individual of a given age at time t and which survive until one time unit later, at time t+1. The components of fecundity thus include reproductive rates and survival rates (the mother must survive from some arbitrary census time to parturition time and the offspring must survive from birth to the next census time).

I use here a formulation of the Leslie model that assumes census immediately after parturition. Thus, the only significant component of survival in the fecundity term is the survival of the mother from census to parturition. Let the first age class be called age class 1 and include individuals which are essentially newborns (remembering that births occurred immediately before census). This convention conforms to a formulation recommended by Goodman (1982).

Fecundity rates can be estimated from resighting data using known-aged individuals. I assume that cows and calves are observed together shortly after parturition. A crude birth rate, b_x, at age x is calculated as the number of calves observed with presumed mothers of age x, divided by all individuals (males and females) of age x. The fecundity rate, f_x, is then estimated as the product of the survival rate of females at a given age and the crude birth rate of the next age class:

$$f_x = p_x b_{x+1} \qquad (1)$$

The population growth rate, e^r, is estimated as the one real-number solution to the discrete-time formulation of Lotka's equation

$$\sum_{x=1}^{\infty} (e^r)^{-x} l_x f_x = 1 \qquad (2)$$

where $l_x = \prod_{i=1}^{x-1} p_i$ = survivorship from birth to age x

(Goodman, 1982). This rate is equivalent to the dominant Eigen value of the Leslie matrix.

Geometric series model

The geometric series model can be thought of as a collapsed form of the Leslie model. The model is named after an arithmetic identity that allows considerable simplification in estimating population growth rates. The number of parameters is reduced to 4 (Table 1): the age at sexual maturation, α; the survivorship from birth to that age, l_α; the mean survival rate of mature animals, p; and the mean fecundity rate of mature animals, m. Goodman (1984) provides a more detailed description of this model. Given the parameters for a Leslie model, it is possible to derive the parameters for the geometric series model. Typically, however, parameters are estimated independently of the Leslie model, and, because fewer parameters are needed, the geometric series model may perform better when sample size is limited. The population growth rate, e^r, is estimated as the solution to the equation

$$e^{r\alpha} - p.e^{r(\alpha-1)} - m.l_\alpha = 0 \qquad (3)$$

(Goodman, 1984).

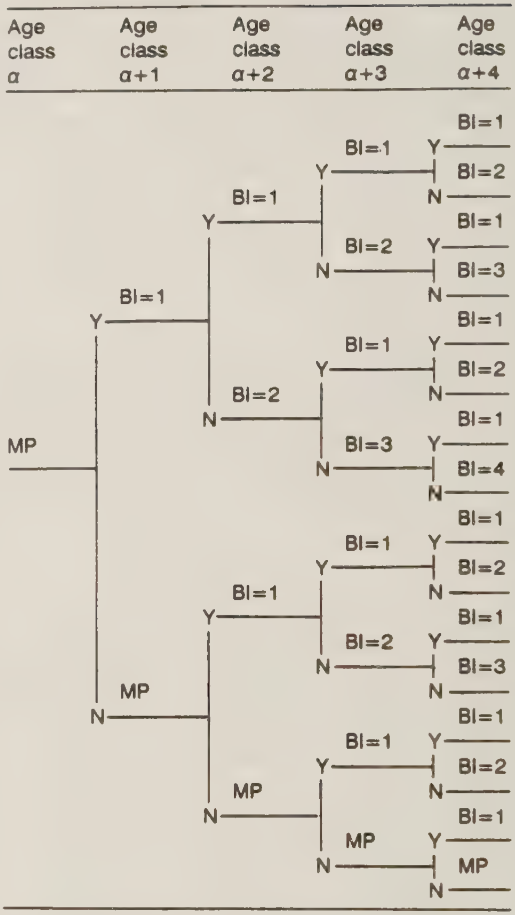

Fig. 1. Illustration of the Markovian method used to estimate Leslie matrix fecundity parameters from first-birth and birth-interval probabilities. Each node represents a decision point. At each node, the probability of having a calf, Y, or not having a calf, N, is given by either the first-birth probability, MP, for that age class (if no prior birth) or the birth-interval probability corresponding to the time, t, since the previous birth (BI=t). The probability of reaching each node is the product of all probabilities leading up to that node. The probability of giving birth for each age class is the sum of the probabilities of all nodes which result in a birth in that age class.

Again, the reproductive parameters of this model can be estimated from resighting data using known-aged individuals. The age at sexual maturation is simply one less than the age class of the youngest individual known to have given birth. The mean crude birth rate is the total number of calves born to known-aged individuals divided by the total number of known-aged individuals in age classes greater than or equal to the age of sexual maturation. The mean fecundity rate is estimated as this mean crude birth rate multiplied by the mean survival rate of mature females.

Birth-interval model

A third model, the birth-interval model, is developed here specifically to deal with the problems encountered using resighting data to estimate birth rates. The reproductive terms include two vectors (Table 1). The first vector, β_x, gives the probability that an individual of age x which has not given birth previously will give birth at age x+1. The second vector, γ_t, gives the probability of giving birth t years following the preceding birth. The first-birth probabilities, β_x, are estimated only from known-aged individuals. The birth-interval probabilities, γ_t, are estimated from all individuals which have given birth previously. Given estimates for these two sets of probabilities, the fecundity terms of a Leslie matrix can be estimated using Markov probability chains (Fig. 1). At this stage, population growth rates can be estimated as described above for the Leslie matrix.

First-birth and birth-interval probability vectors are estimated using iterative maximum-likelihood procedures. Birth-interval probabilities are estimated first. Calves are defined as young-of-the-year. An individual which is seen with a calf in one year can be classified in subsequent years as being in one of three states: (1) seen with a different calf; (2) seen without a calf; or (3) not seen at all. This information can be tabulated as given in Table 2. The probability, Pr(t,j), of being in state j (of the three states given above) at time t after the birth of a calf can be calculated given estimates of the birth-interval probabilities (described above), the probability of being seen in a given year, and the mean survival rate. The likelihood of obtaining the aggregate sample is the product of the likelihoods of each individual observation. The likelihood function is thus

$$L = \prod_{t=1}^{\infty} \prod_{j=1}^{3} (Pr(t,j))^{n(t,j)} \qquad (4)$$

where

t = time since previously seen with calf,
j = observation state at time t and
n(t,j) = number of individuals observed in state j at time t.

Table 2

Examples of the data used to estimate birth-interval probabilities. Values represent the number of individuals seen with a calf, seen without a calf, or not seen, as a function of time since a previous calf.

	Time since previous birth									
	0	1	2	3	4	5	6	.	.	.
No. with calf	195	76	70	70	68	60	61	.	.	.
No. without calf		23	30	25	22	34	24	.	.	.
Not seen		96	95	100	105	101	110	.	.	.

The probability of being seen in a subsequent year is assumed to decrease each year at a rate equal to one minus the mean survival rate. Furthermore, it is assumed that the mean survival rate and the probability of being seen have been estimated using standard mark-recapture techniques. The iterative approach to maximum likelihood proceeds as follows. First, a 'guess' is made for the birth-interval probabilities and the likelihood of the observed aggregate sample is calculated. Next, small changes are made to the estimates of birth-interval probabilities and the likelihood function is re-evaluated. This procedure is repeated until the values are found for birth-interval probabilities that maximise the likelihood function. In practice, I used the simplex algorithm to maximise the natural logarithm of the likelihood function. To reduce the number of parameters estimated, Pr(t,j) was assumed to be constant for all t greater than three.

Table 3

Examples of data used to estimate first-birth probabilities. Values represent the number of known-aged individuals seen with or without a calf as a function of their age. The first reproductive age class is denoted as α.

	Age class										
	1	2	.	.	.	α	$\alpha+1$	$\alpha+2$	.	.	.
No. with calf	0	0	.	.	.	11	50	28	.	.	.
No. without calf	517	424	.	.	.	112	48	42	.	.	.

A similar approach was used to estimate first-birth probabilities. For each year they are observed, known-aged individuals can be classified in one of two states: (1) seen with a calf; or (2) seen without a calf. This information can be tabulated as given in Table 3. The probability of an individual of age x being with a calf, Pr(x,1), is given by the crude birth rate, b_x. The probability of being without a calf, Pr(x,2), is given as the complement of this rate, $1 - b_x$. The likelihood of observing an aggregate sample is the product of likelihoods of each individual observation. The likelihood function is thus

$$L = \prod_{x=1}^{\infty} \prod_{j=1}^{2} (Pr(x,j))^{n(x,j)} \qquad (5)$$

where

x = age of individual
j = observation state at age x
n(x,j) = number of individuals observed in state j at age x.

Again, an iterative approach was used to find the maximum likelihood values for first-birth probabilities. First, a 'guess' is made for the probabilities of having a first calf at each age. These first-birth probabilities and the birth-interval probabilities estimated earlier are used to calculate the expected crude birth rates. The likelihood of the observed aggregate sample is calculated. Next, small changes are made to the estimates of first-birth probabilities and the likelihood function is re-evaluated. This procedure is repeated until the values are found for first-birth probabilities that maximise the likelihood function. Again the simplex algorithm was used to maximise the natural logarithm of the likelihood function. To reduce the number of parameters estimated for this study, Pr(x,j) was assumed to be constant for all x greater than $\alpha+2$.

Monte Carlo simulations

Computer simulations were used to test the bias and precision of the birth-interval model relative to the more familiar Leslie and geometric series models. Simulations used full demographic stochasticity in which transition probabilities (birth or death) were applied to individuals. Initially a sample of n individuals was drawn from a population with known first-birth and birth-interval probabilities and known survival rates. The age distribution of the sample was drawn randomly with respect to the stable age distribution of that population. For each individual, the simulation program had variables to indicate age and sex and, for females, time since the previous birth. This initial population was then projected t time units into the future. At each time step, the probability of dying was evaluated for each individual. At each time step, the probability of having an offspring survive until the next time step was evaluated for each female. New births were distributed randomly among males and females.

A simulation of the process of sighting individuals was superimposed on this stochastic population projection. All individuals were assumed to have the same probability of being seen. At each time step, each individual was randomly assigned as being seen or not being seen based on this probability. A new calf was classified as being seen if its mother was seen. Individuals were classified as known-aged only if they were seen as calves.

Population growth rates were estimated using simulated sightings data collected over t years and using the Leslie, geometric series and birth-interval models. This process was repeated for 40 iterations, and the mean and variance in the resulting population growth rates were calculated for each of the three models.

Conditions for the simulations were designed to cover a feasible range of study conditions. The length of the simulated studies, t, ranged from 10 to 20 years. Values for the simulated population size, n, ranged from 100 to 200 individuals. Values for the probability of being seen ranged from 0.5 to 1.0. Birth-interval and first-birth probabilities and survival rates were chosen to be representative of a stable population of a marine mammal with a lifespan of approximately 20 years (Table 4, Fig. 2). Variations on this life table included increasing birth rates to yield a population growth rate, e^r, of 1.025 (Table 5), and increasing birth and survival rates to yield a population growth rate of 1.062 (Table 6).

Table 4

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 0.998. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.75	0.00	0.66	0.00
2	0.90	0.00	0.74	0.00
3	0.90	0.00	0.80	0.00
4	0.90	0.00	0.84	0.04
5	0.90	0.10	0.88	0.23
6	0.90	0.50	0.91	0.37
7	0.90	0.90	0.93	0.36
8	0.90	0.95	0.94	0.37
9	0.90	1.00	0.95	0.37
10	0.90	1.00	0.95	0.37
11	0.90	1.00	0.95	0.37
12	0.90	1.00	0.94	0.37
13	0.90	1.00	0.92	0.36
14	0.90	1.00	0.89	0.35
15	0.90	1.00	0.86	0.34
16	0.90	1.00	0.80	0.31
17	0.90	1.00	0.73	0.29
18	0.90	1.00	0.63	0.25
19	0.90	1.00	0.51	0.20
20	0.90	1.00	0.00	0.00

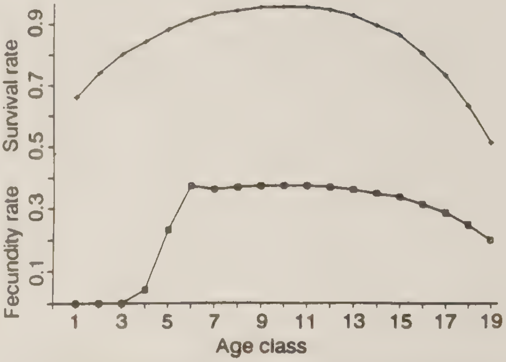

Fig. 2. Fecundity rates and survival rates used in simulation studies. Fecundity rates are as defined by first-birth and birth-interval probabilities (Table 4) and result in a population growth rate of 0.998. It is assumed that the survival rate of age-class 20 is zero.

Table 5

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 1.025. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.90	0.00	0.66	0.00
2	1.00	0.00	0.74	0.00
3	1.00	0.00	0.80	0.04
4	1.00	0.10	0.84	0.23
5	1.00	0.50	0.88	0.40
6	1.00	0.90	0.91	0.41
7	1.00	0.95	0.93	0.42
8	1.00	1.00	0.94	0.43
9	1.00	1.00	0.95	0.43
10	1.00	1.00	0.95	0.43
11	1.00	1.00	0.95	0.43
12	1.00	1.00	0.94	0.43
13	1.00	1.00	0.92	0.42
14	1.00	1.00	0.89	0.40
15	1.00	1.00	0.86	0.39
16	1.00	1.00	0.80	0.36
17	1.00	1.00	0.73	0.33
18	1.00	1.00	0.63	0.29
19	1.00	1.00	0.51	0.23
20	1.00	1.00	0.00	0.00

RESULTS

The mean population growth rates estimated from simulations are given in Table 7 for each of the three models. The expected population growth rate (based on the underlying survival and fecundity schedules) and the realised mean growth rates of the populations are also given. Standard errors in the estimation of population growth rates are given in Table 8 for each of the three models.

Table 6

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 1.062. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.90	0.00	0.75	0.00
2	1.00	0.00	0.80	0.00
3	1.00	0.00	0.85	0.04
4	1.00	0.10	0.87	0.23
5	1.00	0.50	0.89	0.40
6	1.00	0.90	0.91	0.41
7	1.00	0.95	0.93	0.42
8	1.00	1.00	0.94	0.43
9	1.00	1.00	0.95	0.43
10	1.00	1.00	0.95	0.43
11	1.00	1.00	0.95	0.43
12	1.00	1.00	0.94	0.43
13	1.00	1.00	0.92	0.42
14	1.00	1.00	0.89	0.40
15	1.00	1.00	0.86	0.39
16	1.00	1.00	0.80	0.36
17	1.00	1.00	0.73	0.33
18	1.00	1.00	0.63	0.29
19	1.00	1.00	0.51	0.23
20	1.00	1.00	0.00	0.00

Table 7

Population growth rates estimated from Monte Carlo simulations based on three methods for estimating birth rates. Expected growth rates were determined by the underlying survival and birth rates.

Expected growth rate	Prob. being seen	Study period	Sample size	Realized growth rate	Birth-interval model	Leslie matrix model	Geometric series model
0.998	0.5	10	100	1.003	0.992	1.009	0.997
		20	200	0.995	0.994	0.989	0.993
	1.0	10	100	0.997	0.993	0.984	0.979
		20	200	0.997	0.997	0.993	0.995
1.025	0.5	20	200	1.024	1.023	1.024	1.030
	1.0	20	200	1.023	1.025	1.028	1.032
1.062	0.5	20	200	1.054	1.059	1.061	1.062
	1.0	20	200	1.054	1.060	1.063	1.063

In general, biases in the estimation of population growth rates are small for all three models. Mean growth rates from each of the three models (Table 7) differ from the mean realised growth rates by less than the standard error of the estimates (Table 8).

The precision of the three models in estimating population growth rates shows a consistent order. The standard errors for the birth-interval model are consistently lower than those for the geometric series model, which are lower than those of the Leslie matrix model (Table 8). All methods perform better with higher population growth rates. This improved performance is probably a result of greater sample size (although all simulations started with the same population size, a growing population would have more simulated sightings over the course of the study).

Because the simulation study was stochastic, the realised growth rates did not exactly equal the growth rate characteristic of the underlying life table (Table 7). Deviations from the expected growth rates were small, however, indicating no systematic biases in the construction of the simulation model. It is interesting to note that the standard error of estimated growth rates from the birth-interval model is, in most cases, smaller than the standard error of the realised population growth rate.

Table 8

Standard errors of population growth rates estimated from Monte Carlo simulations based on three methods for estimating birth rates. Expected growth rates were determined by the underlying survival and birth rates.

Expected growth rate	Prob. being seen	Study period	Sample size	Realized growth rate	Birth-interval model	Leslie matrix model	Geometric series model
0.998	0.5	10	100	0.017	0.024	0.034	0.027
		20	200	0.010	0.009	0.020	0.015
	1.0	10	100	0.017	0.019	0.039	0.024
		20	200	0.009	0.004	0.015	0.010
1.025	0.5	20	200	0.008	0.004	0.017	0.015
	1.0	20	200	0.010	0.002	0.010	0.008
1.062	0.5	20	200	0.008	0.006	0.014	0.013
	1.0	20	200	0.008	0.003	0.008	0.007

DISCUSSION

The purpose of this paper was to test the relative bias and precision of three methods for estimating reproductive rates from individual resighting data. The simulation study was not intended to estimate accurately the precision that should be expected in the application of these methods to data collected in the field. Survival rates were assumed to be known in the simulation and would have to be estimated if these methods were applied to field data. Simulations did, however, cover a range of sample sizes and study durations that are attainable or have been attained in field studies.

Leslie matrix model

The assumptions of the Leslie matrix model are the least restrictive of the three models considered here. The primary assumption (common to all three models) is that the sample of individuals that are sighted is representative of the population being studied. Estimation of reproductive rates for the Leslie model does not require any implicit assumptions about the age distribution of the population. This advantage may be outweighed by the restrictive numbers of known-aged individuals available for the estimation of reproductive rates. Ages that are greater than the study period will not be represented at all. Given the longevity of cetaceans, very long-term studies may be necessary in order to estimate accurately fecundities for all age classes using the Leslie model.

Geometric series model

The geometric series model shares a common weakness with the Leslie model; birth rates for both are based on small samples of known-aged individuals. Furthermore, when estimating mean birth rate for the geometric series model there is an explicit assumption that the population has a stable age distribution. If, after maturation, birth rates change appreciably with age and if the age distribution is not stable, the estimation of asymptotic population growth rate will be biased. This bias may be small, however, and the lower variance of the geometric series model would make it preferable to the Leslie model in most applications.

Birth-interval model

In estimating birth-interval probabilities, it is assumed that the sample has a stable age distribution. If not, and if birth-interval probabilities change with age, the resulting estimate of population growth rate will be biased. In addition to this assumption (which was the same for the geometric series model) there is the additional assumption that the probability of being seen is the same for all individuals. Based on previous field studies, this is almost certainly not true. Although the mean probability of being seen may be estimated very accurately, individual heterogeneity in sighting probability can lead to serious biases. (This is separate from the assumption that the probability of being seen is independent of the presence of a calf, an assumption that was common to all methods.) Additional work is needed to determine whether sighting heterogeneity would bias the estimation of birth-interval probabilities. If this bias is present, it is probably small. The birth-interval model is still likely to be the best approach for estimating reproductive rates from resighting data.

Simulation studies

The simulation studies here do not account for all sources of error and imprecision that are likely to be encountered in estimating growth rates from field data. First (and probably most importantly), I assumed that survival rates were known. Because I wanted to measure the accuracy in estimating reproductive rates, I did not want to add this additional source of random error. Methods for estimating age-specific survival rates from resighting data have not been examined in depth. It is likely that some method of estimating an aggregate survival rate for all age classes (Buckland, 1990) may have to be incorporated into the models presented here. If age-specific rates are not available, estimates of population growth rates may be sensitive to departures from a stable age distribution.

These simulation studies may also have overestimated the number of known-aged individuals that could be obtained in any field study. I assumed that any individual seen as a calf could later be identified as a known-aged individual. It is likely that many young animals have no distinguishing marks and thus would not be recognised as adults. This would affect all three models, but would affect the Leslie and geometric series models more because they are entirely dependent on known-aged individuals.

No attempt was made to analyse the effect of deviations from a stable age distribution on the estimation of population growth rate. Such deviations would affect each model differently. Also, changes in reproductive rates with age were not explicitly modelled. The number of permutations needed to simulate these effects is overwhelming and beyond the scope of this work. Because the Leslie model has fewer assumptions, it would be less affected than would the other models. Whether this advantage would outweigh the disadvantages of this method would depend on the specific application.

Future research

Methods for estimating reproductive rates for each of the three models could benefit from additional studies. For the Leslie model, it is likely that precision can be increased if age groups are lumped into larger age categories. This is especially true for the older age classes for which the sample of known-aged individuals is very small. As age classes are combined, however, the assumption of a stable age distribution becomes important. Simulation studies could be used to examine the trade-offs between greater precision and violations of this assumption.

For the geometric series model, it may be possible to use individuals of known-minimum-age to augment the sample of known-aged individuals in calculating the mean crude birth rates and mean survival rates. This approach could, however, lead to biases. By adding individuals whose minimum age is greater than the age at sexual maturation, the sample may be weighted towards older mature animals. This would introduce a bias if birth rates or survival rates change appreciably with age. [Mean birth rates and survival rates should be estimated as an average of age-specific rates that are weighted by the actual number of individuals in each age class (Goodman, 1984)]. This latter source of bias should be balanced, however, against the likelihood that older individuals would not be represented in the sample at all unless known-minimum-aged individuals are included. This approach deserves further consideration.

For the birth-interval model, the largest problem (alluded to above) is likely to be heterogeneity in the probability of resighting individuals. This problem should be examined using simulation studies.

For all three approaches, simulation studies should be extended to include the estimation of survival rates. Only then could a realistic appraisal be made of the standard error of estimating population growth rates from resighting data. Based on the results presented here, the component of error due to the estimation of reproductive rates is small. The possibilities of estimating population growth rates from resighting data should be viewed with considerable optimism.

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REFERENCES

Buckland, S.T. 1990. Estimation of survival rates from sightings of individually identifiable whales. Paper SC/A88/ID5 (published in this volume).

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.* 119(6):803–23.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. *Rep. int. Whal. Commn* (special issue 6):161–73.

Keyfitz, N. 1977. *Introduction to the Mathematics of Populations with Revisions*. Addison-Wesley Publ. Inc., Reading, Mass. 490pp.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183–212.

Pielou, E.C. 1977. *Mathematical Ecology*. John Wiley & Sons, New York. 385pp.

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Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*) to acute reductions of ambient oxygen

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Cardiorespiratory responses to acute reductions of ambient oxygen were measured in skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*). Prevented from swimming by a spinal injection of lidocaine, fish were placed in seawater flowing at a velocity equivalent to their normal swimming speed. Ventilation volume ($\dot{V}_g$), heart rate, cardiac output, mouth gape, and inspired water and exhalant water oxygen partial pressures (Pi_{O_2} and Pe_{O_2}, respectively) were simultaneously measured during periods of full oxygen saturation (normoxia) and brief (ca. 3–4 min) periods of reduced oxygen (hypoxia). During hypoxia, Pi_{O_2} ranged from 140 to 50 mmHg. $\dot{V}_g$ during normoxia was significantly different in skipjack, yellowfin, and bigeye tunas (6.7, 3.9, and 1.5 $L \cdot min^{-1} \cdot kg^{-1}$, respectively) and paralleled differences in oxygen consumption (740, 455, and 322 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$). All three species were sensitive to Pi_{O_2}, and mild hypoxia ($Pi_{O_2} \approx$ 115 mmHg) elicited significant cardiorespiratory adjustments, including increased mouth gape and $\dot{V}_g$ and reduced heart rate. Cardiac output was maintained until Pi_{O_2} reached 95 mmHg, but at lower oxygen levels it too began to decrease. Therefore, the three tuna species studied appear as sensitive to hypoxia as other marine teleosts and show cardiorespiratory adjustments at Pi_{O_2} values well above those eliciting swimming speed changes.

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Les réactions cardiorespiratoires à des réductions importantes de la concentration d'oxygène ont été mesurées chez la Thonine à ventre rayé, *Katsuwonus pelamis*, l'Albacore à nageoires jaunes, *Thunnus albacares*, et le Thon ventru, *Thunnus obesus*. Immobilisés par une injection de lidocaïne dans la colonne, les poissons ont été placés dans de l'eau de mer circulant à une vitesse équivalente à leur vitesse normale de nage. Le volume respiratoire ($\dot{V}_g$), le rythme cardiaque, le débit cardiaque, l'écartement des mâchoires et les pressions partielles de l'oxygène dans l'eau aspirée et l'eau exhalée (respectivement Pi_{O_2} et Pe_{O_2}) ont été mesurés simultanément durant des périodes de saturation totale en oxygène (normoxie) et durant de brèves périodes (ca. 3–4 min) de réduction de l'oxygène (hypoxie). Durant l'hypoxie, Pi_{O_2} se situait entre 140 et 50 mmHg. Le volume $\dot{V}_g$ dans des conditions normoxiques était significativement différent chez les trois poissons, (6, 7, 3,9 et 1,5 $L \cdot min^{-1} \cdot kg^{-1}$ chez la Thonine, l'Albacore et le Thon, respectivement) et correspondait à des différences dans la consommation d'oxygène (valeurs respectives de 740, 455 et 322 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$). Les trois espèces se sont avérées sensibles à la pression d'oxygène dans l'eau aspirée et une hypoxie légère ($Pi_{O_2} \approx$ 115 mmHg) déclenchait des ajustements cardiorespiratoires importants, notamment une augmentation de l'ouverture de la bouche et du $\dot{V}_g$ et une réduction du rythme cardiaque. Le débit cardiaque restait le même jusqu'à ce que la pression Pi_{O_2} atteigne 95 mmHg, mais, à des concentrations plus faibles d'oxygène, le débit aussi se mettait à diminuer. Les trois espèces étudiées semblent donc toutes trois sensibles à l'hypoxie, comme d'autres téléostéens marins, et subissent des ajustements cardiorespiratoires à des pressions Pi_{O_2} supérieures à celles qui provoquent des changements dans la vitesse de la nage.

[Traduit par la revue]

Introduction

Although some authors believe that pelagic marine fishes do not encounter low ambient oxygen (hypoxia) (Butler and Metcalfe 1983; Shelton et al. 1986), this is simply not true. Oxygen levels in the oceans are not homogeneous but are dependent upon depth, temperature, productivity, and salinity (Riley and Chester 1971), and significant reductions of ambient oxygen do occur at depths normally occupied by tunas (Barkley 1968; Sund et al. 1981). Although ambient oxygen conditions have been used to explain and predict the apparent movements, abundances, and vulnerability to specific types of fishing gear of various tuna species (Green 1967; Ingham et al. 1977; Barkley et al. 1978; Sharp 1978; Hanamoto 1987), there are few direct experimental observations of the responses of tunas to hypoxia. Tolerances of various tunas species are mostly inferred from correlations of fishery statistics and oceanographic data.

Tunas have evolved the anatomical, physiological, and biochemical adaptations necessary to reach exceptionally high maximum aerobic metabolic rates (Brill 1987). Skipjack tuna can achieve an oxygen consumption rate ($\dot{V}o_2$) of approximately 2500 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (Gooding et al. 1981). By comparison, the maximum $\dot{V}o_2$ of other teleosts is about 1000 ± 200 mg

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$O_2 \cdot kg^{-1} \cdot h^{-1}$ (Brett 1972). Because tunas have exceptionally high oxygen demands, it is reasonable to assume they would be highly sensitive to hypoxia.

Tunas are also obligate ram ventilators and rely on forward movement to develop the pressure head necessary to move water past the gills (Brown and Muir 1970; Roberts 1978). To increase ventilation volume ($\dot{V}_g$), tunas must increase one or more of the following: mouth gape, opercular openings, and swimming speed. Dizon (1977) and Gooding et al. (1981) were apparently the first to directly measure the responses of skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) to hypoxia. Skipjack tuna showed an increase in swimming speed when ambient oxygen fell to 4.0 mg $O_2 \cdot L^{-1}$ (Po_2 = 95 mmHg)[3] and definite signs of stress (high swimming speed, large gape, and absence of schooling behavior) below 3.5 mg $O_2 \cdot L^{-1}$ (83 mmHg). Yellowfin tuna subjected to similar conditions failed to show any change in swimming speed at oxygen levels as low as 2.5 mg $O_2 \cdot L^{-1}$ (59 mmHg). These results suggest that yellowfin tuna are either much more tolerant to hypoxia than are skipjack tuna and other teleosts (Davis 1975) or that they respond to hypoxia in a manner that obviates the need to increase swimming speed.

The efficacy of the cardiorespiratory system of tunas is important in determining their responses to hypoxia. Unfortunately, cardiorespiratory data previously available for tunas have come from fish either anesthetized, paralyzed, or stressed from recent handling (Stevens 1972; Graham and Laurs 1982; Brill 1987; Lai et al. 1987). Furthermore, in all these experiments, $\dot{V}_g$ was set by the experimenter rather than by the fish. Because fixing $\dot{V}_g$ can have important effects on cardiovascular and respiratory functions, our objectives were to develop a system that would allow the simultaneous measurement of several cardiorespiratory variables during normoxia and hypoxia in tunas controlling their own $\dot{V}_g$. This would then allow us to quantify the responses of tunas to acute hypoxia and determine whether physiological abilities could account for reported differences in behavioral responses to hypoxia and differences in the oceanographic distributions of bigeye tuna (*Thunnus obesus*), yellowfin tuna, and skipjack tuna (Sharp 1978; Hanamoto 1987).

Materials and methods

Skipjack, yellowfin, and bigeye tunas were purchased from local commercial fishermen and maintained in continuous-flow outdoor seawater tanks (temperature 25 ± 2°C; salinity 33‰) at the Kewalo Research Facility (Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration). Animal procurement, handling, and maintenance procedures at this facility are described in Nakamura (1972), Queenth and Brill (1983), and Chang et al. (1983). Food was presented daily, but fish were not fed for approximately 20 h prior to use in an experiment. In 3 years, only three bigeye tuna became available for this study because they are only rarely caught by the boats returning fish to the laboratory. The size ranges of the fish used were 0.665–1.000, 0.579–1.278, and 1.900–2.175 kg for skipjack, yellowfin, and bigeye tunas, respectively.

Anesthesia, surgical, and data collection procedures

Initial anesthesia was induced by guiding fish into a plastic bag containing 1.0 $g \cdot L^{-1}$ of tricaine methanesulfonate (MS 222)[4] buffered with 1.0 $g \cdot L^{-1}$ $NaHCO_3$ (the complete technique is described in Jones et al. 1986)). The animal was then placed on a surgical table and force-ventilated with recirculated oxygenated seawater (cooled to 22°C and containing 0.1 $g \cdot L^{-1}$ MS 222) during the 20–40 min required to mount a Doppler blood-flow probe, dye injection and sampling catheters, and electrocardiogram (ECG) wires.

At the conclusion of surgery, but before the fish recovered from anesthesia, a 6 cm long, 20-gauge hypodermic needle was pushed through the dorsal body surface and down into the spinal column. The initial point of needle insertion was immediately lateral to the second spine of the first dorsal fin. Approximately 0.2 mL of a local anesthetic (2% lidocaine hydrochloride) was then injected directly into the spinal cord. This procedure paralyzed all the spinal motor nerves but left all cranial nerves intact. The syringe needle was left in place for subsequent injections.

The fish was then placed under a concave plastic holding device that fit over its dorsal surface and was held in place by two Velcro straps encircling its body. The holder was secured by a series of stainless steel bars bolted to the surface of the surgical table. The fish was positioned so that its snout was directly in front of the roughly rectangular (ca. 2.3 × 3.3 cm) seawater inflow pipe (Fig. 1) and could therefore set its own $\dot{V}_g$.

Seawater exited the pipe at approximately 77 $cm \cdot s^{-1}$ (35 $L \cdot min^{-1}$), which is similar to the normal swimming speeds (60–80 $cm \cdot s^{-1}$) of the tunas used in this study (Magnuson 1978). Fish were therefore provided with ample water flow, at a velocity that permitted a normal $\dot{V}_g$ to be achieved with a mouth gape similar to that observed in swimming fish. Fish were allowed 1–2 h to recover before the first hypoxic trial was begun.

As shown in Fig. 1, air-saturated seawater was mixed with deoxygenated seawater (Po_2 = 20 mmHg) to achieve an initial Po_2 of 50 mmHg (2.1 mg $O_2 \cdot L^{-1}$). Pure oxygen was bubbled through a gas-exchange column to bring the inflow seawater Po_2 (Pi_{O_2}) to full saturation (152–157 mmHg or 6.4–6.6 mg $O_2 \cdot L^{-1}$). A gas flowmeter controlled the amount of oxygen flowing to the column and enabled us to set the Pi_{O_2} anywhere between 140 and 50 mmHg (5.9–2.1 mg $O_2 \cdot L^{-1}$), with no change in water flow rate. Pi_{O_2} was continuously monitored with a Radiometer Po_2 electrode mounted in a temperature-controlled flow-through cuvette and calibrated with standard zero solution and air-saturated seawater. The electrode was connected to a Radiometer PHM 71 blood gas analyzer. Cuvette temperature was maintained the same as that of the inflowing seawater. All experiments were conducted at 25 ± 1°C.

$\dot{V}_g$ was measured with a dye dilution technique developed by Jones et al. (1990). Exhalant water (Pe_{O_2}, i.e., the water stream exiting the opercular openings) was sampled with two PE-50 catheters sutured through the posterior medial edge of each opercular opening about 0.5 cm ventral to the pectoral fin insertion. The ends of the catheters projected approximately 3 mm into the gill cavity and were under the opercular covers. Dye concentrations in exhalant water were determined spectrophotometrically. $\dot{V}_g$ was calculated by averaging the transmittances of the water samples from left- and right-side catheters (see Appendix for explanation).

Cardiac output was measured with a Parks model 806A directional Doppler blood flowmeter. A flat transcutaneous flow probe was fixed with tissue adhesive to the area inside the gill cavity overlying the ventral aorta. The probe was positioned 0.3–0.7 cm anterior to the bulbus arteriosus – ventral aorta junction and did not interfere with gill arch or opercular movements. Mean cardiac output was obtained by passing the pulsatile cardiac output signal through a low-pass filter. Attempts to calibrate the flow probe postmortem by infusing blood past the probe at a known flow rate were generally unsuccessful. Therefore, cardiac output measurements were recorded in arbitrary units on the basis of a known zero flow. (Zero flow was recorded between heartbeats during hypoxic bradycardia.) Heart rate was recorded with a

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[3] Oxygen levels in water may be expressed either as partial pressure (mmHg) or as concentration (mg $O_2 \cdot L^{-1}$). Partial pressure and concentration are linearly related through the factor of oxygen solubility. Oxygen solubility is, in turn, affected by temperature and salinity. Whenever possible, oxygen levels will be given in both units.

[4] Use of trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

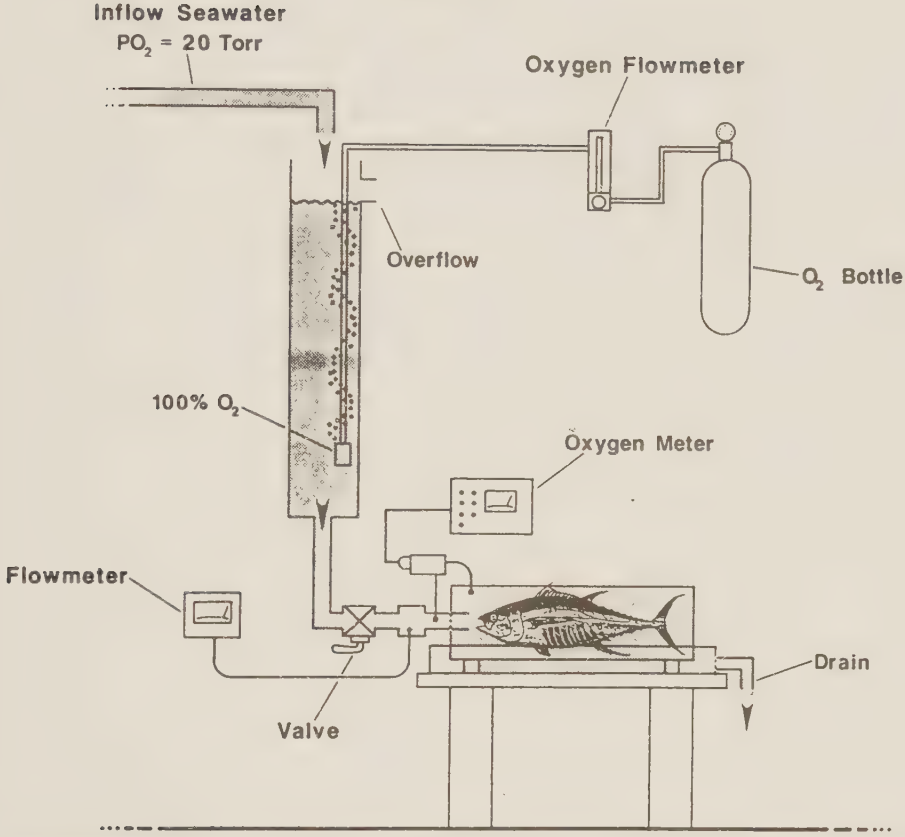

FIG. 1. Experimental apparatus for exposing tunas to hypoxia. The concave plastic holder, fitted to the fish's back, and the series of stainless steel bars holding the plastic holder and fish are not shown (1 Torr = 133.322 Pa).

cardiotachometer triggered by the ECG signal. ECG electrodes were mounted subcutaneously near the heart. Stroke volume was calculated by dividing cardiac output by heart rate.

Mouth gape, taken as the vertical distance from the tip of the snout to the lower jaw, was measured directly with a ruler fixed to the side of the seawater inflow pipe. Dynamic changes in gape were recorded with an impedance converter and electrodes glued to the lateral surfaces of the lower and upper jaws. Outputs from the cardiotachometer, Doppler flowmeter, impedance converter, and ECG amplifier were recorded on a six-channel pen recorded.

Pe_{O_2} was measured with the same Radiometer blood gas analyzer and oxygen electrode used to monitor Pi_{O_2}. Utilization (U) was calculated from Pi_{O_2} and Pe_{O_2} as

$$[1] \quad U = [(Pi_{O_2} - Pe_{O_2})/Pi_{O_2}] \cdot 100$$

Oxygen consumption ($\dot{V}O_2$, in mg $O_2 \cdot h^{-1}$) was calculated with the Fick method:

$$[2] \quad \dot{V}O_2 = \dot{V}_g (Pi_{O_2} - Pe_{O_2}) \cdot \alpha$$

where $\dot{V}_g$ is the ventilation volume ($L \cdot h^{-1}$) and α is the solubility of oxygen (mg $O_2 \cdot L^{-1} \cdot$ mmHg) at the experimental temperature and salinity.

Experimental procedure

Tuna were exposed to brief periods (ca. 3–4 min) of hypoxia (140–50 mmHg or 5.9–2.1 mg $O_2 \cdot L^{-1}$) presented in a random sequence of 10-mmHg steps. Gape, heart rate, cardiac output and Pi_{O_2} were recorded continuously. Dye was infused and samples of exhalant water (control measurements) were taken during the normoxic period immediately preceding onset of hypoxia. Dye infusion was then stopped, and Pi_{O_2} reduced to a preselected level. Two minutes after Pi_{O_2} had stabilized, dye infusion was begun again and samples of exhalant water were taken (hypoxia measurement). Pi_{O_2} was then brought back to full saturation. A 15-min intertrial period was allowed, during which time Pe_{O_2} and dye concentrations were measured.

Statistical methods

Interspecific comparisons of control measurements (excluding cardiac output and stroke volume) were made using analysis of variance (ANOVA) and multiple-range tests. All values are expressed as mean ± standard error.

Because not every fish completed all 10 trials, dividing the data into 10-mmHg ranges resulted in an inadequate number of samples in some ranges. Data were therefore combined into 20-mmHg ranges (144–125, 124–105, 104–85, 84–65, 64–45 mmHg). To determine whether any of the variables (i.e., $\dot{V}_g$, gape, heart rate, or relative cardiac output) measured in hypoxia differed significantly ($P < 0.05$) from their counterparts in normoxia, control measurements in a particular range were compared with their respective hypoxia values with a paired Student's *t*-test ($P < 0.05$).

To graph the effects of hypoxia, changes in gape, $\dot{V}_g$, heart rate, cardiac output, and stroke volume were calculated as the fractional change from the control measurements that immediately preceded hypoxia. Data were grouped into intervals based on Pi_{O_2}.

TABLE 1. Cardiorespiratory variables in skipjack, yellowfin, and bigeye tunas and rainbow trout

	Skipjack tuna	Yellowfin tuna	Bigeye tuna	Rainbow trout^a
Mass (kg)	0.841 ± 0.4 (10)	1.07 ± 0.09 (10)	2.03 ± 0.07 (3)	0.9–1.5
$P\mathrm{i}_{\mathrm{O}_2}$ (mmHg)	153.0 ± 0.5 (10)	152.5 ± 0.5 (10)	154.5 ± 0.2 (3)	153
Gape (mm)	8.2 ± 0.9^b (10)	5.9 ± 1.0^c (9)	9.7 ± 1.7 (3)	—
$\dot{V}_g$ ($\mathrm{L\cdot min^{-1}}$)	5.5 ± 0.9 (10)	4.1 ± 0.7 (8)	3.1 ± 0.2 (3)	—
$\dot{V}_g$ ($\mathrm{L\cdot min^{-1}\cdot kg^{-1}}$)	6.7 ± 1.0^b (10)	3.9 ± 0.4^c (8)	1.5 ± 0.2^d (3)	0.21 ± 0.06
$P\mathrm{e}_{\mathrm{O}_2}$ (mmHg)	101.9 ± 6.6 (9)	93.3 ± 7.9 (7)	74.8 ± 2.1 (3)	101
U (%)	33.5 ± 4.4 (9)	39.0 ± 4.9 (7)	51.6 ± 1.4 (3)	33.0 ± 0.5
$\dot{V}\mathrm{O}_2$ ($\mathrm{mg\ O_2\cdot kg^{-1}\cdot h^{-1}}$)	740 ± 103 (9)	455 ± 66 (7)	323 ± 33^d (3)	49.9 ± 0.9
Heart rate (beats/min)	117 ± 12 (10)	99 ± 6 (10)	99 ± 18 (3)	70 ± 3

NOTE: Values are given as mean ± SD, with number of fish in parentheses.
[a] Trout in fresh water at 10°C, data are from Kiceniuk and Jones (1977).
[b] Statistically different ($P < 0.05$) from yellowfin tuna.
[c] Statistically different ($P < 0.05$) from bigeye tuna.
[d] Statistically different ($P < 0.05$) from skipjack tuna.

Results

Normoxia

Mean normoxia values for all three tuna species are given in Table 1. Data for rainbow trout, *Salmo gairdneri* (Kiceniuk and Jones 1977), have been added for comparison. Total $\dot{V}_g$ is not significantly different in the three species. However, when standardized by weight, skipjack tuna had a significantly higher $\dot{V}_g$ than yellowfin tuna, which in turn had a significantly higher $\dot{V}_g$ than bigeye tuna. $\dot{V}\mathrm{O}_2$ of skipjack tuna was not significantly different from that of yellowfin tuna, but both were higher than that of bigeye tuna. $P\mathrm{e}_{\mathrm{O}_2}$, U, and heart rates were not significantly different in the three species.

Hypoxia

Figure 2 presents a chart record of the dynamic cardiorespiratory responses of a yellowfin tuna when $P\mathrm{i}_{\mathrm{O}_2}$ was reduced to 90 mmHg ($3.8\ \mathrm{mg\ O_2\cdot L^{-1}}$). Various physiological adjustments are apparent within seconds after the onset of hypoxia and the increase in $P\mathrm{i}_{\mathrm{O}_2}$ at the conclusion of hypoxia. (Note that there was an approximately 10-s lag in the response of the electrode measuring seawater $P\mathrm{O}_2$; the tracings in Fig. 2 have not been corrected for this lag.) The responses to hypoxia included an increase in gape (and presumably $\dot{V}_g$) and a reduction in heart rate with little decrease in cardiac output until $P\mathrm{i}_{\mathrm{O}_2}$ fell below 100 mmHg ($4.2\ \mathrm{mg\ O_2\cdot L^{-1}}$).

Yellowfin and skipjack tunas appeared to respond to the rate of change as well as to the absolute change in $P\mathrm{i}_{\mathrm{O}_2}$. When the flow of oxygen to the gas-exchange column was reduced, $P\mathrm{i}_{\mathrm{O}_2}$ decreased exponentially. Therefore, when $P\mathrm{i}_{\mathrm{O}_2}$ was reduced from 155 to 50 mmHg (6.5–$2.1\ \mathrm{mg\ O_2\cdot L^{-1}}$), for example, the initial rate of change of $P\mathrm{i}_{\mathrm{O}_2}$ was more rapid than when the reduction was from 155 to 140 mmHg. As a result, we found that fish would not respond to a change in $P\mathrm{i}_{\mathrm{O}_2}$ from 155 to 140 mmHg, but would respond within the first few seconds of the start of a change to 50 mmHg, after $P\mathrm{i}_{\mathrm{O}_2}$ had decreased to only 140 mmHg ($5.9\ \mathrm{mg\ O_2\cdot L^{-1}}$). However, data recorded while $P\mathrm{i}_{\mathrm{O}_2}$ was changing were not used to determine sensitivity to hypoxia because of the difficulty in establishing the exact response time of the seawater $P\mathrm{O}_2$ electrode.

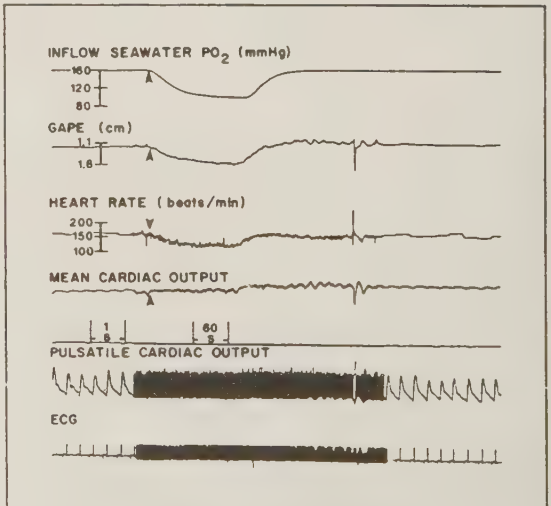

FIG. 2. A chart record of the cardiorespiratory response of a yellowfin tuna to hypoxia. Note that the changes in gape and heart rate parallel those of inflow seawater $P\mathrm{O}_2$ ($P\mathrm{i}_{\mathrm{O}_2}$). Cardiac output was maintained by an increase in stroke volume until the $P\mathrm{i}_{\mathrm{O}_2}$ fell below approximately 100 mmHg ($4.2\ \mathrm{mg\ O_2\cdot L^{-1}}$).

Figure 3 shows that, in skipjack tuna, no changes in the measured variables occurred until $P\mathrm{i}_{\mathrm{O}_2}$ fell to 124–105 mmHg (5.2–$4.4\ \mathrm{mg\ O_2\cdot L^{-1}}$), at which point gape and $\dot{V}_g$ had

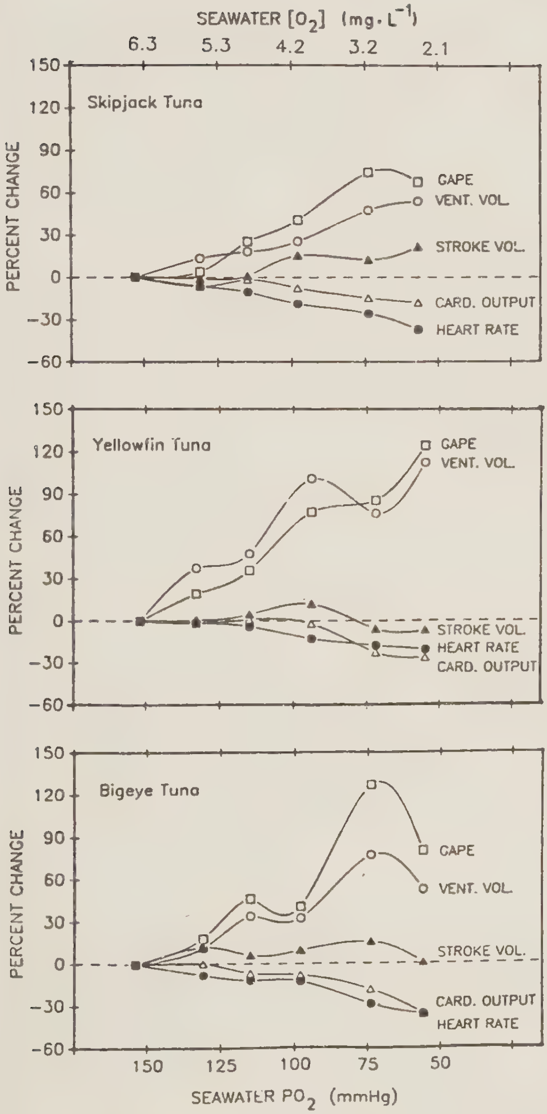

FIG. 3. Cardiorespiratory response to acute hypoxia in skipjack, yellowfin, and bigeye tunas. Data are mean percent change from the values measured during the control periods immediately preceding the hypoxic episodes. The inflow seawater Po_2 values are the averages of each range. Standard error bars have been omitted for clarity.

increased significantly (Table 2, Fig. 3). Heart rate and cardiac output decreased significantly while stroke volume increased significantly at the next level of hypoxia (104–85 mmHg, 4.4–3.6 mg $O_2 \cdot L^{-1}$). With the exception of relative stroke volume at 84–65 mmHg (3.5–2.7 mg $O_2 \cdot L^{-1}$), all measured variables in all three tuna species remained significantly different from control values as hypoxia became more severe.

In yellowfin tuna, gape and $\dot{V}_g$ increased and heart rate decreased at the same level of hypoxia as in skipjack tuna (Table 2, Fig. 3). Yellowfin tuna were able to maintain cardiac output at control levels until Pi_{O_2} fell to 84–65 mmHg (3.5–2.7 mg $O_2 \cdot L^{-1}$). Stroke volume was not significantly different from control values.

Bigeye tuna showed significant increases in gape when Pi_{O_2} fell to 124–105 mmHg (5.2–4.4 mg $O_2 \cdot L^{-1}$) (Fig. 3). No other changes were recorded until Pi_{O_2} fell to 104–85 mmHg (4.4–3.6 mg $O_2 \cdot L^{-1}$), by which point cardiac output was significantly reduced. There were no additional reductions in heart rate until Pi_{O_2} reached 84–65 mmHg (5.2–4.4 mg $O_2 \cdot L^{-1}$). $\dot{V}_g$ and stroke volume did not change significantly at any level of hypoxia. However, the P value was 0.06 for $\dot{V}_g$ at 124–105 mmHg (5.2–4.4 mg $O_2 \cdot L^{-1}$) and below. The large increase in gape and $\dot{V}_g$ at 74 mmHg (3.1 mg $O_2 \cdot L^{-1}$) (Fig. 3) was heavily influenced by one animal whose gape and $\dot{V}_g$ increased 230 and 134%, respectively.

When Pi_{O_2} was reduced below 70 mmHg (3.0 mg $O_2 \cdot L^{-1}$), Pe_{O_2} occasionally equalled Pi_{O_2}. Probably because of the large gape, opercular flare, or increased $\dot{V}_g$, the exhalant-water catheter could have been sampling water that passed through the gill cavity but did not come into contact with the secondary lamellae (and therefore did not exchange oxygen with the blood). While this was seen only during the most severe hypoxia, we have chosen not to report any Pe_{O_2} values and associated calculations (U and $\dot{V}o_2$) measured during hypoxia.

Discussion

Experimental techniques

Ideally, physiological studies of the cardiorespiratory system of obligate ram-ventilating fishes should be conducted on fish swimming in either a tank or a water tunnel. Water tunnels, suitable for use with large active fishes such as tunas, are difficult to design and extremely expensive to build. Although some water tunnel studies have been performed successfully on albacore (*Thunnus alalunga*) (Graham and Laurs 1982; Graham et al. 1989), such studies using skipjack or yellowfin tuna have thus far met with little success (Brill and Dizon 1979). Regardless of whether tuna are swimming in a tunnel or a tank, our experience is that they are unable to tow multiple cannulae or leads for more than a few hours. This makes it virtually impossible to measure several cardiorespiratory variables simultaneously. The spinal block preparation was developed specifically to circumvent these problems and provide a method for studying multiply instrumented, unanesthetized fish for prolonged periods.

The use of a spinal block to inhibit swimming motions appears to be a suitable technique for use with tunas. The local anesthetic selectively inhibits the spinal nerves controlling swimming muscle activity while leaving cranial nerves intact. Fish were able to control their own $\dot{V}_g$ by adjusting mouth gape and opercular openings in response to changes in Pi_{O_2}. Regular eye movements and pectoral fin extension (in response to lateral tilting) also were noted. Each 0.2-mL injection of lidocaine hydrochloride was effective in blocking swimming movements for approximately 1–3 h, and fish appeared to remain in good condition for up to 10–12 h. The only side effect was a transitory (2–3 min) increase in heart rate following injection.

An effectively similar spinal transection technique has been used in a number of physiological studies on brook trout, *Salvelinus fontinalis* (McKim and Goeden 1982), and rainbow trout (McKim and Heath 1983; McKim et al. 1987). These investigators found no significant differences in heart rate, respiratory rate, ventilation volume, oxygen utilization, or oxygen consumption when fish spinally transected at the eighth

TABLE 2. Summary of statistically significant (at $P < 0.05$) changes in physiological variables at different levels of hypoxia

Oxygen level: mmHg	Oxygen level: mg $O_2 \cdot L^{-1}$	Gape	Ventilation vol. ($\dot{V}_g$)	Heart rate	Cardiac output	Stroke volume
144–125	6.1–5.3	ns	ns	ns	ns	ns
124–105	5.2–4.4	SYB	SY	ns	ns	ns
104–85	4.3–3.6	SYB	SY	SY	SB	S
84–65	3.5–2.7	SYB	SY	SYB	SY	ns
64–45	2.6–1.9	SYB	SY	SYB	SYB	S

NOTE: S, significant in skipjack tuna; SY, significant in skipjack and yellowfin tunas; SYB, significant in skipjack, yellowfin, and bigeye tunas; ns, not significant.

vertebra were compared with untransected animals. Moreover, McKim and Goeden (1982) also found that the respiratory responses of transected fish to hypoxia closely follow those of restrained but unoperated salmonids.

Because tunas will not survive the normal ≥24-h postoperative recovery period used with more docile and well-studied cyprinid or salmonid species, we decided to use measurement techniques that were as minimally invasive and disruptive to normal ventilation as possible. We chose not to use a rubber membrane sewn around the mouth to separate $P\mathrm{i}_{O_2}$ and $P\mathrm{e}_{O_2}$, as is normally done with salmonids (Davis and Cameron 1971). The anatomy of tunas makes this procedure difficult because the ventral opercular openings extend anteriorly almost to the tip of the lower jaw. Also, for obligate ram-ventilating fishes a substantial pressure head would have to be provided to force water over the gills. We believe these procedures could significantly affect $\dot{V}_g$ in normoxia and the changes in $\dot{V}_g$ occurring during hypoxia. Measuring $P\mathrm{e}_{O_2}$ by catheterization does have its limitations (Davis and Watters 1970), but it has been successfully used to study the responses of rainbow trout to hypoxia (Holeton and Randall 1967). Moreover, the adequacy of our methodology is supported by the fact that our metabolic rate measurements, which are dependent on accurately measuring $\dot{V}_g$ and U, agree closely with those from swimming tunas studied by Boggs (1984) and Jones et al. (1989).

Our use of a flat, transcutaneous Doppler flow probe also represents a compromise. It required no invasive surgery, but we could not calibrate the flow probe postmortem, and only data on relative changes (i.e., control versus hypoxia) could be obtained. "Cuff-type" transducers, which fix vessel diameter and provide a fixed relationship between blood velocity and volume flow rate, would have been better. Unfortunately, the area surrounding the bulbus arteriosus – ventral aorta of tunas is highly vascularized (Williams 1976). This resulted in extensive bleeding when attempts were made to mount Doppler flow cuffs. Furthermore, we believe that incisions to expose the bulbus arteriosus – ventral aorta could damage the muscles and nerves used for opening the lower jaw and, therefore, interfere with control of ventilation. This is an especially acute problem, since the tunas could be given only 1–2 h to recover from surgery.

Normoxia

The $\dot{V}_g$ of skipjack tuna in normoxia (6.7 $L \cdot min^{-1} \cdot kg^{-1}$) was higher than the 5 $L \cdot min^{-1} \cdot kg^{-1}$ predicted by Langille et al. (1983), based on data collected by Gooding et al. (1981). The U value (33%) at this high flow rate was similar to that reported for rainbow trout (Kiceniuk and Jones 1977), which have a much lower $\dot{V}_g$ (Table 1). Stevens (1972) measured U at 71% in anesthetized and artificially ventilated skipjack tuna, probably because $\dot{V}_g$ was set at an extremely low level (2.8 $L \cdot min^{-1} \cdot kg^{-1}$).

Mean $\dot{V}O_2$ values of skipjack and yellowfin tunas in our study were higher then those of fish immobilized with the neuromuscular blocker Flaxedil (gallamine triethiodide) (Brill 1987). Apparently, immobilization by spinal block results in more metabolic activity than immobilization by neuromuscular block. The metabolic rates of our spinally blocked skipjack and yellowfin tunas are closer to the routine metabolic rates of the same species measured by Boggs (1984). Mean $\dot{V}O_2$ values of skipjack tuna in our study were also similar to those of lightly anesthetized (immobile) skipjack tuna (Stevens 1972). No metabolic rate data are currently available for bigeye tuna.

Mean heart rates of our skipjack and yellowfin tunas were substantially lower than the 203 and 137 beats/min, respectively, measured in neuromuscularly blocked fish (Brill 1987). Stevens (1972) found a mean heart rate of 70 beats/min (range 46–142 beats/min) in anesthetized skipjack tuna, but this is likely due to the fact that the fish were significantly underventilated. Kanwisher et al. (1974) found telemetered heart rates of swimming skipjack tuna to be 80–240 beats/min. No data are currently available on the heart rate of bigeye tuna.

Regardless of the differences among the three tuna species used in this study (the $\dot{V}_g$ values of skipjack tuna were about 72 and 350% higher than those of yellowfin and bigeye tunas, respectively), the $\dot{V}_g$ values of tunas are much higher than the 200–900 $mL \cdot min^{-1} \cdot kg^{-1}$ of other teleosts and elasmobranchs (Johansen 1982). This is probably a reflection of the higher standard metabolic rates of tunas (Brill 1979, 1987; Gooding et al. 1981; Graham et al. 1989).

Hypoxia

Skipjack, yellowfin, and bigeye tunas were all sensitive to hypoxia. The onset of cardiorespiratory adjustments was rapid and lasted for as long as hypoxia ensued. In a few instances when hypoxia was prolonged for 5–8 min, bradycardia and increased gape were maintained until normoxia was resumed, suggesting that responses were not transient. The immediate cardiorespiratory adjustments to hypoxia are suggestive of an oxygen sensor in the gill (Bamford 1974), rather than in the central nervous system, which would have been indicated by more delayed responses (i.e., 1–2 min following the onset of hypoxia) (Saunders and Sutterlin 1971; Hughes 1978). In vitro nerve recordings from the first gill arch of yellowfin tuna showed bursting patterns sensitive to the $P\mathrm{O}_2$ of both the external bathing solution and the perfusion fluid (Milsom and

Brill 1986), though the responses to changes in the Po_2 of the perfusion fluid were much more rapid. These results also suggest the presence of an internal oxygen receptor in the gill.

The majority of teleosts studied to date increase $\dot{V}_g$ during hypoxia. Maximum increases in $\dot{V}_g$ range from 200 to 600% (Hughes and Saunders 1970; Shelton et al. 1986). The maximum increases in $\dot{V}_g$ were only 50 and 100% in skipjack and yellowfin tunas, respectively, representing an increase to about 7–10 $L \cdot min^{-1} \cdot kg^{-1}$. While the relative changes in $\dot{V}_g$ may be modest, because of the enormous $\dot{V}_g$ during normoxia, the absolute increases in $\dot{V}_g$ of tunas far exceed those of other fishes.

The increase in $\dot{V}_g$ in response to hypoxia, although similar in sensitivity, varied in magnitude in the three species. Yellowfin tuna showed a much larger percent increase in gape and $\dot{V}_g$ than did skipjack tuna. This may be a reflection of the yellowfin tuna's lower $\dot{V}_g$ in normoxia, which allows a larger fractional increase. In view of the bigeye tuna's relatively low $\dot{V}_g$ in normoxia, one might expect to see large changes in gape and $\dot{V}_g$ in response to hypoxia. However, the increases in $\dot{V}_g$ and gape were relatively small, being more similar to those of skipjack tuna than to those of yellowfin tuna. Data on depth distributions (Hanamoto 1987; Holland et al. 1990) suggest that bigeye tuna may be relatively more hypoxia tolerant, which may explain our results. They are a far deeper-living species than skipjack or yellowfin tuna, and often occur at depths where Po_2 is 100 mmHg (4.9 mg $O_2 \cdot L^{-1}$) or less. Further studies on this species are clearly indicated.

The different $\dot{V}_g$ values obtained during normoxia may also explain the different behavioral responses of skipjack and yellowfin tunas to hypoxia. The former abruptly increase swimming speed at an ambient Po_2 below 90 mmHg (3.8 mg $O_2 \cdot L^{-1}$), whereas the latter maintain a constant swimming speed even at an ambient Po_2 below 50 mmHg (2.1 mg $O_2 \cdot L^{-1}$) (Dizon 1977). Because skipjack tuna are apparently limited in their ability to increase $\dot{V}_g$ by increasing gape (because of their relatively larger $\dot{V}_g$ during normoxia), they may have to increase swimming speed to generate the required flow. Yellowfin tuna, by virtue of their larger scope for changes in gape, may be able to compensate for hypoxia to a greater degree without changing swimming speed.

In most teleosts, a reduction in ambient Po_2 causes a reduction in heart rate (bradycardia), but no change in cardiac output because of concomitant increases in stroke volume (Randall 1982). While hypoxic bradycardia was recorded in all three tuna species, increases in stroke volume in skipjack tuna were ineffective in maintaining relative cardiac output. The inability of skipjack tuna to maintain cardiac output may have been a result of the experimental setup, however. Spinally blocked fish may lack the benefit of increased venous return resulting from tail flexion, although the contribution of tail movement to venous return is a matter of debate (Satchell 1971; Jones and Randall 1978; Farrell 1984). A statistically significant increase in stroke volume was never recorded in yellowfin or bigeye tuna.

Davis (1975) reviewed the literature, grouped teleosts by environment, and calculated the "incipient oxygen response threshold" (which he defined as "the oxygen level where some organism just starts to respond in some way to reduced oxygen availability"). The mean incipient oxygen response thresholds were 85.6 ± 5.4 (SE) mmHg (5.3 ± 0.4 mg $O_2 \cdot L^{-1}$) and 111 ± 31 mmHg (6.7 ± 2.1 mg $O_2 \cdot L^{-1}$) for freshwater and marine species, respectively. All three tuna species showed significant increases in gape at Pi_{O_2} values between 124 and 105 mmHg (5.2–4.4 mg $O_2 \cdot L^{-1}$), and skipjack and yellowfin tunas showed increases in $\dot{V}_g$ at this level of hypoxia. Tunas therefore appear to be as sensitive to hypoxia as other marine teleosts.

Our experiments give insight into the responses of tunas in the laboratory, but their responses in less restricted environments should be considered. Our study clearly shows that skipjack and yellowfin tunas are equally sensitive to hypoxia and that the latter respond physiologically at hypoxia levels more moderate than those needed to elicit swimming speed changes. Presumably cardiorespiratory changes in response to hypoxia are aimed at maintaining the oxygen delivery to the tissues. Increased swimming speed must therefore be considered a "last resort" because of its high energetic cost. The lack of a behavioral response in tunas is not necessarily an accurate indicator of the animals' sensitivity to or tolerance of hypoxia.

Acknowledgments

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Appendix

Ideally, when a dye dilution technique is used to measure $\dot{V}_g$, the dye should be completely mixed within the mouth. If this is achieved, any opercular sampling site will suffice. Unfortunately, complete mixing is not always achieved without a mechanical stirring device mounted within the fish's mouth. However, doing this would negate the main advantages of a dye dilution system for measuring $\dot{V}_g$ in ram-ventilating fish: it is simple, light enough to be useful in swimming fish, and minimally disruptive to normal ventilatory processes.

When there are unequal dye concentrations exiting each operculum, the data can be corrected by averaging the transmittances, although this is not an intuitively obvious solution. The only required assumption is that flow rates of water exiting both opercula are equal. To the best of our knowledge, it has never been shown for any fish species whether the flow rates of water from each operculum are equal or unequal; however, equal water flow has been assumed in other studies on ventilation volume in teleosts (e.g., Lomholt and Johansen 1979).

Unequal dye concentrations in the exhalant water can be modeled as a system with one inflow but with separate outflows and separate dye injection points. The following variables are needed to describe this system:

$\dot{V}_{gT}$ is total water inflow
$\dot{V}_{gl}$ is water outflow through the left branch (operculum)
$\dot{V}_{gr}$ is water outflow through the right branch (operculum)
$\dot{V}_{dyeT}$ is total dye inflow

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Growth During the Larval and Juvenile Stages of the Northern Anchovy, *Engraulis mordax*, in the California Current During 1980–84

John L. Butler

ABSTRACT: Increment widths and back-calculated growth rates for northern anchovy, *Engraulis mordax*, did not differ during the years 1980–84. This evidence of stable larval growth rates does not support the theory that it is the variation in larval growth rates that directly affects the magnitude of recruitment. Furthermore, since growth rates remained stable, even though zooplankton volumes in 1983 were well below the long-term mean, it follows that surviving post-first-feeding larval anchovies may not be food limited.

The size of juvenile northern anchovy was reduced during the 1982–83 El Niño "phenomenon" in the California Current. Mean lengths of anchovy juveniles collected in the fall were greatest in 1980, least in 1982, and intermediate in 1981, 1982, and 1984. Growth rates back calculated from otolith increment widths did not differ significantly between the 1980 and 1983 cohort, until 100 days after first feeding. Reduced growth after 100 days largely determined the smaller size of 1983 anchovy juveniles. Condition factor was also reduced in the 1983 cohort. The 1982 cohort was not greatly affected, because El Niño did not have a pronounced effect off the North American coast until well after the 1982 northern anchovy spawning season.

Through the years, the overall abundance of many pelagic fishes varies with the strength of individual year class; changes in mortality rates early in life (Hjort 1914, 1926), rather than parent stock size, may determine the size of individual year classes. Considerable controversy, however, surrounds details of the exact stage and mechanism through which changes in individual year-class strength occur.

The co-occurrence of fish larvae and their food is a mechanism that has been proposed to explain variations in year-class strength (Hjort 1914, 1926). Lasker (1978) has shown that food availability may affect survival of first-feeding northern anchovy, *Engraulis mordax*, larvae in the sea. Food availability may not affect the survival beyond the first-feeding stage; however, Methot (1981) found that early larval anchovy growth rates in the sea were the same as those of well-fed, laboratory-reared larvae. Survival through the larval stage does not determine the magnitude of the northern anchovy recruitment (Peterman and Bradford 1986; Peterman et al. 1988). Thus food availability for larvae may not determine the year-class strength and whether food availability affects juvenile survival are yet to be investigated.

A simulation model of the northern anchovy population indicates that the growth rate of late larvae and early juveniles may affect the magnitude of recruitment (Smith 1985). If mortality rates in the marine environment are size-specific, as predicted by Peterson and Wroblewski (1984), and if growth rates determine the duration of the most vulnerable stages, reduced growth should adversely affect survival. The extent to which growth rates of late larvae and juveniles vary is unknown.

The growth rate of juveniles also affects adult size. Off southern Baja California, the adult size of northern anchovy is entirely determined by juvenile growth, because these fish show no growth after 18 months (Parrish et al. 1985). Analysis of the regional patterns of growth of northern anchovy shows that the average length of fish at a given age increases from south to north. The length at 18 months ranges from 101.1 mm off southern Baja California to 126.6 mm off central California (Parrish et al. 1985).

Because batch fecundity is a function of body size in broadcast spawners, the juvenile and adult growth rates determine the reproductive capacity over the adult lifespan. Competition among juveniles for resources affects adult fertility in other species (Prout and McChesney 1985), and, if growth of juvenile pelagic fishes is food limited, competition among juveniles may

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be a mechanism of density-dependent compensation.

Growth rates of larval and juvenile anchovy during El Niño periods are of particular interest, because the growth rates during an environmental perturbation may reveal details of the processes of growth and survival during normal conditions. During the 1982–83 El Niño event off California, temperatures were elevated (Lynn 1983; Simpson 1983) and zooplankton density was reduced in 1983 (McGowan 1985). If planktivorous fish compete for food, competition should be highest when zooplankton abundance is lowest. Comparison of growth rates throughout the larval and juvenile stages during periods of low and high food abundance may show the size range at which the larval or the juvenile stage is most important. In this paper I examine the interannual variability in growth rates of anchovy larvae and juveniles during periods of low and high food abundance.

METHODS

Samples of juveniles from the central population of northern anchovy were obtained from midwater trawl hauls taken in 1980–84 by the Sea Survey Program of the California Department of Fish and Game. Annual cruises to monitor the strength of the incoming year class of northern anchovy have been conducted during September and October since 1976; Mais (1974) has described the gear and sampling procedures. The surveys extended along the Pacific coast from central Baja California to Point Conception, CA, with the exception of 1982, when the southern limit was the U.S.-Mexican border. Trawl hauls were taken nearshore inside of a 75 fm contour where young of the year are most abundant during the fall (Parrish et al. 1985).

Twenty five juvenile northern anchovy were randomly taken from each positive trawl haul and frozen for age determination. A subsample of 200 juvenile anchovy was randomly taken from the 800 to 1,000 fish collected on each survey for analysis of growth rate using daily increments in the otoliths. Fish were measured from the tip of the snout to the posterior edge of the hypural plate (standard length), and otoliths were removed and mounted on microscope slides using Eukitt[1] mounting medium.

Growth rates and ages of juvenile northern anchovy were determined by counting and measuring daily increments in the otoliths (Methot 1981). The increment widths were measured and recorded along a transect from the focus to the posterior margin of the otolith (otolith radius), using a video-coordinate digitizer connected to a microcomputer. The otoliths were progressively polished between readings, using 15 and 0.3 μ lapping film, to reveal increments along the entire transect. Data from different areas of the otolith were collected as the increments became visible. During each reading groups of 10 or less (typically five) increments were counted and measured. The number of increments measured was reduced if width varied among increments.

ANALYSIS AND RESULTS

Data from both otoliths and several replicate transects per otolith were combined to calculate age and otolith increment widths (Methot 1981). Mean increment width was calculated at each point along the radius from the focus to the posterior margin of the otolith. In some cases, it was impossible to obtain measurements of all increment widths in the otoliths. In these cases, increment widths were interpolated using linear approximation (see Methot 1983 for details). Data for increment widths and age estimates were not used if more than 5% of age was calculated from interpolated increments.

A direct comparison of the average size of recruits from year to year is inappropriate because their ages may differ from year to year owing to differences in the dates of spawning (Methot 1983) or to dates of collection. To eliminate this bias, the dates of hatching were determined from the dates of sampling and ages, and fish were grouped by year and month of hatching.

Interannual and seasonal differences in length were tested, using an analysis of covariance (Bartlett et al. 1984) with age as the covariate. This analysis adjusted the mean length to the grand mean age of 208 days, approximately the time elapsed from the peak of spawning to the date of capture. Since the relation of length to age is typically nonlinear, some error is introduced using a linear adjustment. The difference in dates of sampling is, however, only about one month and the relation of size to age is approximately linear from two to six months.

Analysis of covariance of these data indicates parallel lines with differences in means (Case 2c in Bartlett et al. 1984). Thus, comparison of lengths adjusted by age between years of fish hatched during the same calendar month is reliable. Comparison of lengths of fish hatched at the extremes of the same spawning season may be less reliable than between-year comparisons. Fish hatched in January are four months older than fish hatched in May, and linear extrapolation to a common age may introduce error. However, since growth is decelerating, linear extrapolation overestimates mean lengths of fish hatched at the extremes of the spawning season. The fact that lengths of fish hatched in January and May in all years, except 1983, are less than lengths of fish hatched in March indicates that the error is not great.

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[1] Reference to tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.

The allometric relations of length and weight to otolith radius were estimated using nonlinear regression. These relations were used to back-calculate age-specific size and growth rates for individual fish; not all fish were weighed in 1980 and 1981, and data were pooled from 1980 to 1982 to determine the allometric relations of both length and weight to otolith radius. Individual relations were determined for 1983 and 1984.

The growth rates in length and in weight were determined from increment widths and the first derivative of the empirical relationship of fish size and otolith radius. The condition factor (dry weight/length cubed) was significantly less in anchovy juveniles collected in 1983 than in anchovy juveniles collected in 1980–82. Therefore, the algorithm to convert otolith increment size to growth in dry weight differed among years. The equation used to calculate growth in length was

$$\Delta L/\Delta t = (\Delta R/\Delta t)(\Delta L/\Delta R); \qquad (1)$$

where $\Delta R/\Delta t$ is rate of change of the width of the daily increments, and $\Delta L/\Delta R$ is the slope of the observed relationship of fish length and otolith radius.

The variance of the product (Y) of two variables (X, Z) is given by

$$\mathrm{Var}(Y) = Z^2\mathrm{Var}(X) + X^2\mathrm{Var}(Z) + 2XZ\,\mathrm{Covar}(XZ) \qquad (2)$$

if the variables are not independent (Goodman 1960). The estimate of the variance of $\Delta R/\Delta t$ was the variance of the measurement of increment width of the fish in each group. If the length, radius relation was linear, the variance of $\Delta L/\Delta R$ was estimated from $S^2_{Y|X}$, the variance of the slope of the regression of length on otolith radius. If the relation of length to radius was nonlinear, as was often the case, the variance of $\Delta L/\Delta R$ was estimated by partial derivatives. The variance of $\Delta W/\Delta R$ was not calculated; the complex derivative may not be a good estimate of the true variance.

The author tested the assumption that the covariance was equal to zero by comparing the slopes of the relations of juvenile fish length and otolith radius for 70–100 mm, slow- and fast-growing fish collected in October 1984 that were ≥ 1 year old. The slope was 0.0419 for anchovy older than one year and 0.0314 for fish younger than one year old. These slopes were not significantly different ($P > 0.10$, ANCOVA). Consequently confidence intervals around back-calculated growth rates were calculated ignoring the third term in Equation (1).

Lengths of anchovies were significantly different between months and years ($P < 0.01$, ANCOVA). Within a spawning season, fish hatched during February, March, and April grew faster than fish hatched in January or May (Fig. 1), although this was not evident for the 1983 or 1984 data. The mean of five fish in January 1982 was not different from that of the April 1982 sample. The adjusted lengths of juveniles collected from the 1983 year class where less than the adjusted lengths of any of those from 1980–82 for all months but May (Fig. 1, Table 1). The adjusted lengths of juveniles from

TABLE 1.—Mean lengths at capture of juvenile northern anchovy hatched in various months of 1980–84, adjusted to a common age of 208 days. SE and *N* stand for standard error and number of fish, respectively.

	Month of Hatching				
Year	Jan.	Feb.	Mar.	Apr.	May
1980	71.4	78.7	84.6	83.6	72.3
SE	3.6	1.6	1.0	1.6	
N	7	30	104	33	2
1981	77.0	79.9	83.5	82.7	79.7
SE	2.2	2.2	1.2	1.5	2.4
N	21	29	42	35	16
1982	81.1	85.79	84.1	81.0	78.9
SE	4.5	1.3	1.1	1.2	1.6
N	2	32	70	53	29
1983	70.0	71.4	71.5	70.8	73.7
SE	2.6	2.1	0.9	0.9	2.7
N	9	17	99	45	8
1984	74.8	77.0	76.0	76.8	75.6
SE	1.5	1.3	1.3	1.9	1.5
N	39	53	42	22	17

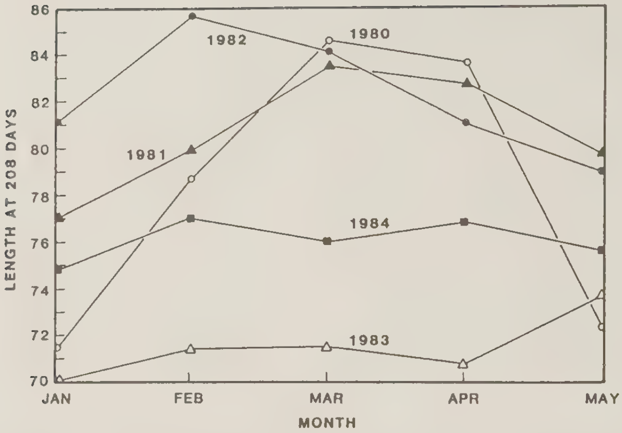

FIGURE 1.—Mean lengths adjusted for age of northern anchovy spawned in 1980–84. For each year, fish are grouped by back-calculated date of hatching, and length at capture is adjusted to mean age of 208 days.

1984 were intermediate between those of 1980–82 and 1983.

Fish hatched during 1983 did not grow more slowly throughout the entire larval and juvenile stage than during other years. Otolith increment widths from 104 juveniles hatched in March 1980 were compared with otolith increment widths from 99 juveniles hatched in March 1983 (Fig. 2). In fish smaller than 40 mm in length, increment width was not different. Above 40 mm, the otolith increment widths were smaller in the 1983 sample than in the 1980 sample ($P < 0.01$); the 95% confidence limits for the two cohorts did not overlap. These results show that the difference in lengths of the two cohorts indicated by the analysis of covariance is largely due to difference in growth rate after a size of 40 mm, rather than to a reduction of growth throughout life.

Back-calculated lengths and growth rates of 1980 northern anchovy juveniles were greater

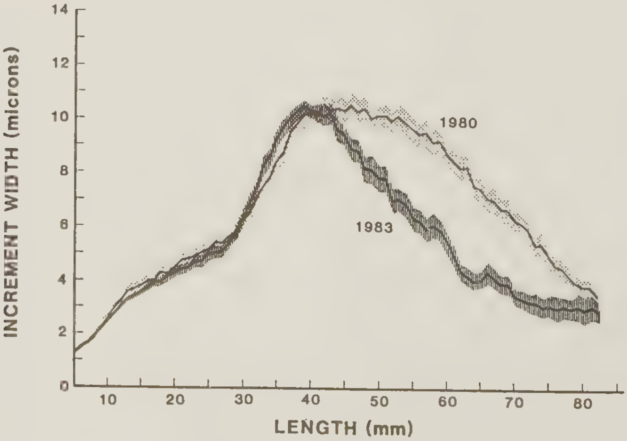

FIGURE 2.—Average otolith increment width versus length of 104 northern anchovy spawned in March 1980 and of 99 anchovy spawned in March 1983. Shaded areas are 95% confidence intervals.

than those of 1983 (Figs. 3, 4). Cohorts did not differ significantly in growth until approximately 40 mm. The age of the end of the late larval (10 mm) period was 20 days in 1980 and 19 days in 1983. A local minimum for growth rates of 1983 fish occurred at about 35 mm and at about 42 mm for growth rates of 1980 fish. This corresponds, approximately, to metamorphosis from late larval stage to juvenile stage. The duration of the late larval period (10–35 mm) was about 70 days in both 1980 and 1983.

After metamorphosis, growth rates increased in 1980 and 1983 until about 40 mm. At about 40 mm, the growth rates of the two cohorts diverged, and the mean back-calculated growth rate of the 1983 cohort was well below the estimated 95% confidence interval of the 1980 cohort. Growth rates declined steadily in 1983 at sizes larger than 40 mm, while growth rates of about 0.4 mm/d were sustained in 1980 until almost 60 mm. After 60 mm, growth declined at about the same rate as the decline in the 1983

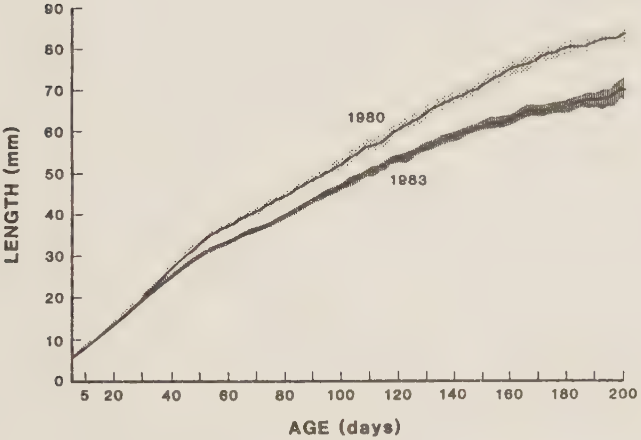

FIGURE 3.—Length versus age of northern anchovy larvae and juveniles of the March 1980 and 1983 cohorts back calculated from daily increments in otoliths.

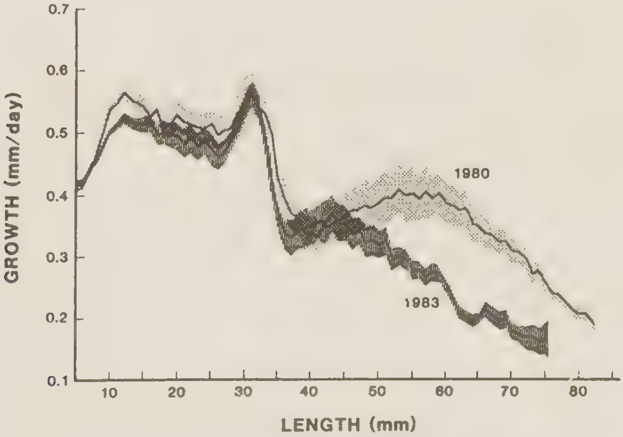

FIGURE 4.—Age-specific growth rates back calculated from daily increment widths of northern anchovy spawned in March 1980 and March 1983. Growth rate of length in mm per day. Shaded areas are 95% confidence intervals.

cohort. Growth within cohorts varied most between 40 and 60 mm.

In 1980 and 1983, northern anchovy growth in weight increased rapidly at small sizes (Fig. 5). Back-calculated growth rates for 1983 reached a local maximum of 6.5 mg/d at about 40 mm and then declined before slowly increasing to 7.5 mg/d at 79 mm. Back-calculated growth rates for 1980 showed a steady increase to about 11.5 mg/d at about 65 mm, which was maintained until about 75 mm, after which growth declined. The growth of northern anchovies hatched in March 1983 peaked at an earlier time (about June) in 1983 and at a smaller size (40 mm), whereas the growth of anchovies hatched in March 1980 peaked near the end of July 1980 and at a larger size at (about 65 mm).

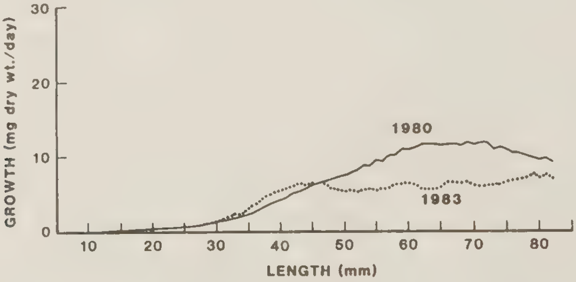

FIGURE 5.—Mean back-calculated growth rates of northern anchovy spawned in March 1980 and March 1983. Growth rate of mass in mg dry weight per day.

DISCUSSION

Growth rates of late larval northern anchovy did not vary in two otherwise extreme years, 1980 and 1983. Methot (1981) found little variance in early larval growth in the sea. Smith (1985) postulated that major changes in recruitment would result from changes in growth rates in the late larval period (10–35 mm) from 0.227 to 0.559 mm/d, a difference of 0.3 mm/d. In this study, however, growth rates of the late larval stage varied by <0.05 mm/d between 1980 and 1983.

Northern anchovy juveniles grew less during 1983 and 1984, compared with the previous three years. Fiedler et al. (1986) also reported reduced growth of anchovy in 1983, but the mean size of 1 yr old fish indicated a dramatic recovery in 1984. This apparent recovery may be in part due to geographic shifts in the population or to changes in spawning date and sampling time in 1984.

When size is adjusted for age and date of spawning, growth of juvenile northern anchovy was reduced in fish hatched in February through April of 1984 compared with fish hatched in the same months in 1980–82 (Fig. 1). This result is consistent with the results from studies of other fish populations on the west coast during El Niño. Growth rates and condition factors were also reduced in the Pacific herring, *Clupea harengus pallasi* (Spratt 1987), the blue rockfish, *Sebastes mystinus* (Van Traskie[2]), and in chinook, *Onchorhynchus tshawytscha*, and coho, *Onchorhynchus kisutch*, salmon (Pearcy and Schoener 1987) during El Niño.

Although the 1982–83 El Nino was fully developed by October 1982 along the coast of Peru, full development of large scale warming off the North American coast did not occur until January 1983 (Lynn 1983). Positive temperature anomalies (>1°C) were evident both at the surface and at depth throughout the California Current (McGowan 1985; Norton et al. 1985). Negative salinity anomalies associated with subsurface temperature anomalies indicated intrusion of low salinity water from the south and west into the Southern California Bight (Simpson 1983).

These temperature anomalies represent a large change in the heat content of the ocean but are small relative to the thermal range of northern anchovy. Thus the small size of juvenile anchovies during 1983 may be a direct result of reduced food availability at the same time that the rapidly growing juveniles experienced higher metabolic rates due to the elevated environmental temperatures. Zooplankton volumes on CalCOFI line 90 (line 90 intersects the coast at lat 33°29.9′N, long. 117°44.4′W and proceeds seaward on a bearing 240° clockwise from North) were lower than the 95% confidence limit of the 30 year CalCOFI time series (McGowan 1985).

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[2] Van Traskie, D. 1985. Growth of blue rockfish (*Sebastes mystinus*) during El Niño. (Abstr.) Calif. Coop. Fish. Invest. Conf., Idyllwild, CA, Oct. 22–25, 1985.

Growth rates were not, however, depressed over the entire early life history. The growth rates of larval stages (5–35 mm) were not significantly different between the two years 1982–83 (Figs. 3, 4). Growth rates in 1983 were reduced in the early juvenile stage, and in particular after 40 mm, compared with growth rates in 1980.

Thus food was not growth limiting until the fish reached a certain size. As fish larvae grow, the ration necessary to sustain growth increases. Since the density of food particles decreases with size (Sheldon and Parsons 1967; Sheldon et al. 1972), at some stage food must become growth limiting. Based on this analysis, food-limited growth is unlikely in anchovies <40 mm during conditions that existed in the Southern California Bight in 1983, and unlikely in anchovies <65 mm during "normal" years such as 1980.

The similarity of back-calculated larval growth rates between years may be a result of the interaction of growth and mortality. A wide range of growth rates are possible at this stage (Hunter 1980), but variable growth rates are not observed in the field. Mortality of slow-growing individuals may reduce the range of growth rates in survivors to metamorphosis.

While the 1957–58 El Niño had a dramatic effect on northern anchovy recruitment in 1958, the numbers of fish in the 1983 and 1984 year classes were not appreciably lower than the previous years (Methot 1988). Thus, although the juvenile period was prolonged in 1983, recruitment was not affected. The major effect of El Niño on the anchovy population was to reduce the size of recruits as well as perhaps the size of adults and the reproductive potential of the 1983 and 1984 cohorts.

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LITERATURE CITED

Bartlett, J. R., P. F. Randerson, R. Williams, and D. M. Ellis.
1984. The use of analysis of covariance in the back-calculation of growth in fish. J. Fish Biol. 24:201–203.

Fiedler, P., R. D. Methot, and R. Hewitt.
1986. Effects of California El Nino 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Goodman, L. A.
1960. On the exact variance of products. J. Am. Statist. Assoc. 55:708–713.

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 20:1–228.
1926. Fluctuations in the yearclasses of important food fishes. J. Cons. int. Explor. Mer 1:5–38.

Hunter, J. R.
1980. Culture and growth of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Lasker, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

Lynn, R. J.
1983. The 1982–83 warm episode in the California Current. Geophys. Res. Let. 10:1093–1095.

Mais, K.
1974. Pelagic fish surveys in the California Current. Calif. Dep. Fish Game Fish Bull. 162:1–79.

McGowan, J. A.
1985. El Niño 1983 in the Southern California Bight. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North, Niño effects in the Eastern Subarctic Pacific Ocean, p. 166–187. Wash. Sea Grant, Seattle, WA.

Methot, R. D.
1981. Growth rates and age distributions of larval and juvenile northern anchovy, *Engraulis mordax*, with inferences on larval survival. Ph.D. Thesis, Univ. California, San Diego, CA, 209 p.
1983. Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.
In press. Synthetic estimates of historical abundance and mortality for northern anchovy. *In* E. F. Vetter and B. A. Megrey (editors), Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. Vol. Ser.

Norton, J., D. McLain, R. Brainard, and D. Husby.
1985. The 1982–83 El Niño event off Baja and Alta California and its ocean climate context. *In* W. S. Wooster and D. L. Fluharty (editors), El Niño North. Niño effects in the Eastern Subarctic Pacific Ocean, p. 44–72. Wash. Sea Grant, Seattle, WA.

Parrish, R. H., D. L. Mallicoate, and K. F. Mais.
1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 83:483–496.

Pearcy, W. G., and A. Schoener.
1987. Changes in the marine biota coincident with the 1982–83 El Niño in the Northeastern Subarctic Pacific Ocean. J. Geophys. Res. 92:14417–14428.

Peterman, R. M., and M. J. Bradford.
1987. Wind speed index correlates with mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science 235:354–366.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot.
1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45:8–16.

Peterson, I., and J. S. Wroblewski.
1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41:1117–1120.

Prout, T., and F. McChesney.
1985. Competition among immatures affects their adult fertility: population dynamics. Am. Nat. 126:521–558.

Sheldon, R. W., and T. R. Parsons.
1967. A continuous size spectrum for particulate matter in the sea. J. Fish. Res. Board Can. 24:909–915.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe, Jr.
1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17:327–340.

Simpson, J. J.
1983. Large-scale thermal anomalies in the California current during the 1982–1983 El Niño. Geophys. Res. Lett. 10:937–940.
1984. El Niño induced onshore transport in the California Current during 1982–1983. Geophys. Res. Lett., 11:241–242.

Smith, P. E.
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42:69–82.

Spratt, J. D.
1987. Variation in the growth rate of Pacific herring from San Francisco Bay, California. Calif. Fish Game 73:132–138.

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Application of the Leslie Model to Commercial Catch and Effort of the Slipper Lobster, *Scyllarides squammosus*, Fishery in the Northwestern Hawaiian Islands

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ABSTRACT—Commercial catch and effort data were fit to the Leslie model to estimate preexploitation abundance and the catchability coefficient of slipper lobster, Scyllarides squammosus, *in the Northwestern Hawaiian Islands (NWHI). A single vessel fished for 34 consecutive days in the vicinity of Laysan Island and caught 126,127 total slipper lobster in 36,170 trap hauls. Adjusted catch of legal slipper lobster dropped from a high of 3.70 to 1.16 lobster per trap haul. Preexploitation abundance at Laysan Island was an estimated 204,000 legal slipper lobster, which was extrapolated to yield an estimate of 1.2 × 10⁶ to 3.8 × 10⁶ lobster for the entire NWHI slipper lobster fishery.*

Introduction

Intensive fishing experiments are widely accepted in fishery literature as a relatively easy way to estimate the catchability coefficients of exploitable stocks. This information can be used to determine absolute estimates of exploitable stock, as compared with relative estimates (i.e., catch per unit effort (CPUE)). The two most widely accepted methods for obtaining these estimates are the Leslie and Delury models, which have been explored in considerable detail (Ricker, 1975; Crittenden, 1983; Schnute, 1983; Polovina, 1986). These models have several assumptions: The population fished is isolated or closed, fishing removals account for all changes in stock size, and catchability is constant (although as shown by Polovina (1986), this assumption is not restrictive). Substantial fishing effort exerted over a short timespan should reveal that the slope of a linear regression of CPUE on cumulative catch (Leslie and Davis, 1939) or LOG (CPUE) on LOG cumulative effort (Delury, 1947) is negative. In the Leslie model, the x-intercept reveals virgin stock size (K), the y-intercept shows initial CPUE at virgin biomass, and the absolute value of the slope of the line is the catchability coefficient (q).

Most of the reported studies using the Leslie model have involved laboratory experiments, fieldwork in ponds, or, more recently, field studies using research vessels at sea (Polovina, 1986; Ralston, 1986). While field studies offer many benefits, they may have operational and financial constraints resulting in relatively small amounts of effort being expended. One way to overcome this problem is to use commercial operations to fish marine reserves or restricted areas. If a commercial vessel fishes in a previously unexploited area for a reasonable amount of time, then removals from the fished stock will be great enough to cause a significant decline in CPUE. Such a situation presented itself in June 1986, when a commercial lobster vessel fished for slipper lobster, *Scyllarides squammosus*, at Laysan Island in the Northwestern Hawaiian Islands (NWHI). Laysan Island, with its associated bank, is a designated reserve for the spiny lobster, *Panulirus marginatus*, and had no prior history of slipper lobster exploitation. The vessel fished for 34 consecutive days and caught over 126,000 slipper lobster. As required by law, the vessel kept daily catch and effort logs for spiny lobster. The same data, along with additional information on trap placement, were maintained for slipper lobster. This otherwise confidential information was released by the vessel owner and skipper to the authors for analysis.

This paper presents a Leslie model modified for the use of commercial fisheries data to estimate catchability and preexploitation abundance of slipper lobster at Laysan Island. This species is distributed throughout the Indo-Pacific region north of Clipperton Island (Williams, 1986). A commercial slipper lobster fishery centered in the NWHI has recently emerged in conjunction with that for spiny lobster. In 1986, over 480 metric tons (t) of slipper lobster, valued at $2.3 million were landed by the NWHI lobster fleet (Clarke[1]). Until this time, estimates of catchability have been made by production models that treat spiny and slipper lobsters as one stock. Here, an independent estimate of slipper lobster alone will be presented, along with an estimate of preexploitation stock size at Laysan Island that may be applied to the entire NWHI lobster fishery.

Methods

The vessel fished between 11 June and 14 July 1986 in the vicinity of Laysan Island and its associated bank, which is

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[1] Clarke, R. P. 1989. Annual report of the 1988 western Pacific lobster fishery. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-89-5, 28 p.

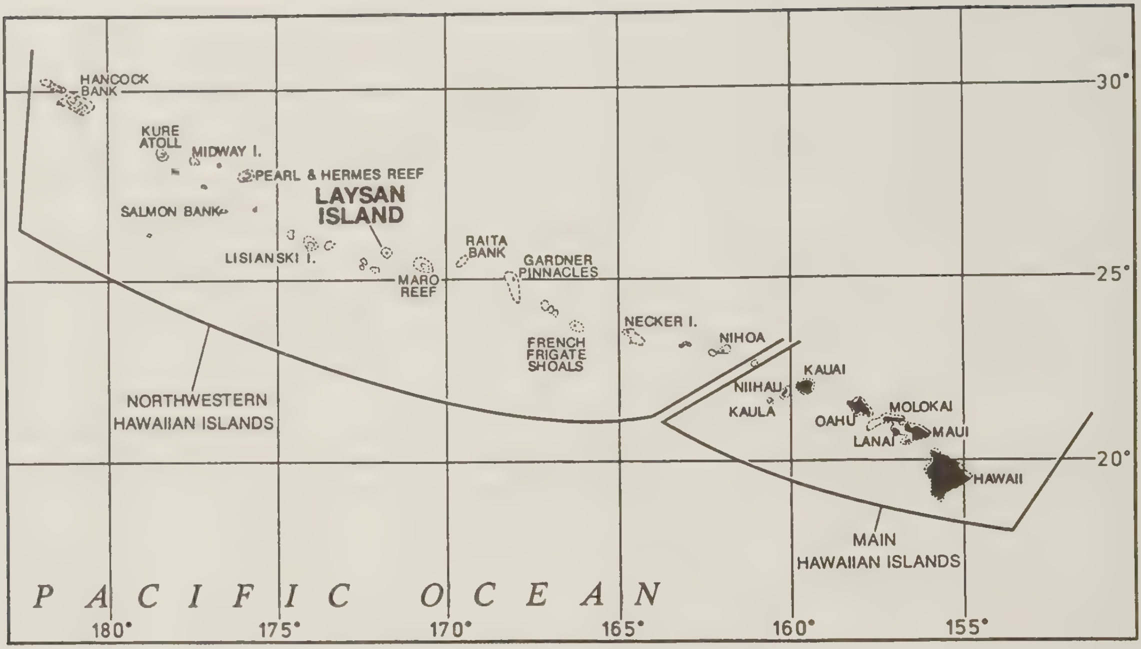
HANCOCK BANK
KURE ATOLL
MIDWAY I.
PEARL & HERMES REEF
LAYSAN ISLAND
SALMON BANK
LISIANSKI I.
RAITA BANK
GARDNER PINNACLES
MARO REEF
NECKER I.
NIHOA
FRENCH FRIGATE SHOALS
NORTHWESTERN HAWAIIAN ISLANDS
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
MAIN HAWAIIAN ISLANDS
PACIFIC OCEAN
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1.—The Northwestern Hawaiian Islands, including Laysan Island.

henceforth referred to as Laysan bank. Laysan Island is a small, uninhabited, predominantly coral-sand island, 2.8 km long and 1.7 km wide. It is located at lat. 25°42′N and long. 171°44′W, at the midpoint of the NWHI (Fig. 1), and is about 1,350 km northwest of Honolulu. The bank includes 482.2 km^2 (horizontal planar area) of potential habitat for lobster at the 20-200 m depths (WPRFMC[2]). Slipper lobster are known by NWHI fishermen to concentrate in areas at the 40-120 m depths.

The daily operations of the vessel involved deploying and hauling 1,125 Fathom Plus[3] lobster traps set in strings spaced at 30 m intervals. The traps are of black polyethylene construction (overall dimensions, 104 × 81 × 46 cm) and have two tapered entrance funnels (30 cm exterior diameter; 50 × 50 mm mesh). They were fished in 7 strings of about 160 traps each and baited with Pacific mackerel, *Scomber japonicus*. Strings were soaked overnight and retrieved the following day; therefore, the standard unit of effort is the trap-haul. The northwest corner of Laysan bank was initially explored for lobster concentrations at 30-120 m depths; however, some traps were set as deep as 200 m.

In 1986, there were no Federally mandated laws for slipper lobster. However, because of market conditions, the vessel retained only those slipper lobster that were free of eggs and had a tail size larger than 85 g (3 ounces), returning all others to the water. The vessel counted retained lobster but estimated the egg-bearing lobster and those below the 85 g minimum size. Since that time, a minimum size regulation of 56 mm tail width has been applied to the slipper lobster (WPRFMC[4]). The 56 mm tail width closely approximates the 85 g slipper lobster tail size (National Marine Fisheries Service (NMFS) unpubl. data); therefore, retained lobster can be viewed as legal lobster, those below 85 g as sublegal, and egg-bearing females as berried.

The general Leslie model is written as

$$U\langle t\rangle = q(K - CC\langle t\rangle); \qquad (1)$$

where $U\langle t\rangle$ is the CPUE at the time t, q is the catchability coefficient, K is preexploitation stock size, and $CC\langle t\rangle$ is the cumulative catch at time t. If slipper lobster are partitioned into legal, sub-

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[2] Western Pacific Regional Fishery Management Council (WPRFMC). 1983. Spiny lobster fishery management plan. Western Pacific Regional Fishery Management Council, Honolulu, Hawaii, 213 p.

[3] Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Western Pacific Regional Fishery Management (WPRFMC). 1987. Crustacean fishery management plan amendment 5. Western Pacific Regional Fishery Management Council, Honolulu, Hawaii, 58 p.

Table 1.—Summary of catch and effort data from a commercial vessel fishing for slipper lobster at Laysan bank, Hawaii, 11 June through 14 July 1986. Legal lobster have tails >85 g, sublegal are <85 g, and berried are egg-bearing females. Catch per unit effort (CPUE) equals number of legal lobster per trap-haul.

	Lobster catch				Adjusted cumulative legal catch	Daily effort	CPUE
Day	Legal	Sublegal	Berried	Total			
1	2,133	1,000	1,000	4,133	1,066.5	1,125	1.896
2	1,675	450	600	2,725	2,970.5	1,125	1.488
3	2,976	1,785	1,050	5,811	5,296.0	1,125	2.645
4	3,788	1,850	1,580	7,218	8,678.0	1,125	3.367
5	2,883	1,750	1,150	5,783	12,013.5	1,125	2.562
6	2,430	1,470	980	4,880	14,670.0	1,125	2.160
7	4,092	2,400	1,600	8,092	17,931.0	1,125	3.637
8	3,267	1,800	1,200	6,267	21,610.5	1,125	2.904
9	3,440	1,000	1,500	5,940	24,964.0	1,125	3.057
10	2,790	820	450	4,060	28,079.0	1,125	2.480
11	2,418	740	500	3,658	30,683.0	1,125	2.149
12	2,112	420	300	2,832	32,948.0	1,125	1.877
13	2,325	340	150	2,815	35,166.5	805	2.888
14	2,325	320	190	2,835	37,491.5	805	2.888
15	2,976	450	325	3,751	40,142.0	805	3.696
16	2,232	360	380	2,972	42,746.0	805	2.772
17	2,670	380	340	3,390	45,197.0	805	3.316
18	3,680	810	580	5,070	48,372.0	1,125	3.271
19	2,362	425	260	3,047	51,393.0	1,125	2.099
20	2,142	400	300	2,842	53,645.0	1,125	1.904
21	1,955	290	235	2,480	55,693.5	1,125	1.737
22	1,924	210	135	2,269	57,633.0	1,125	1.710
23	2,332	320	280	2,932	59,761.0	1,125	2.072
24	1,216	145	205	1,566	61,535.0	645	1.885
25	2,158	235	150	2,543	63,222.0	1,125	1.918
26	2,328	380	230	2,938	65,465.0	1,125	2.069
27	2,612	575	210	3,397	67,935.0	1,125	2.321
28	2,332	480	245	3,057	70,407.0	1,125	2.072
29	2,605	545	310	3,460	72,785.5	1,125	2.315
30	2,312	510	210	3,032	75,334.0	1,125	2.055
31	2,046	325	290	2,661	77,513.0	1,125	1.818
32	2,280	385	250	2,915	79,676.0	1,125	2.026
33	2,523	387	268	3,178	82,077.5	1,125	2.242
34	1,308	175	95	1,578	83,993.0	1,125	1.162
Total	84,647	23,932	17,548	126,127		36,170	

legal, and berried categories, equation (1) can be rewritten as

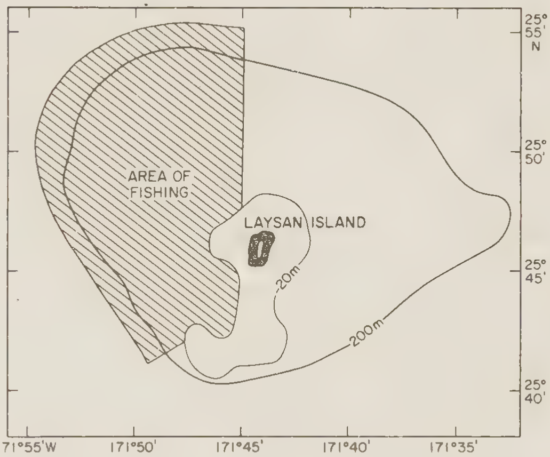
$$U_l + U_s + U_b = q_l(K_l - CC_l) + q_s(K_s - CC_s) + q_b(K_b - CC_b); \quad (2)$$

where the subscripts l, s, and b correspond to the legal, sublegal, and berried categories. During the intensive fishing at Laysan bank, sublegal and berried slipper lobster were returned after capture. To eliminate inaccuracies associated with the possibility of returned lobster being recaptured, only the legal terms in equation (1) were used:

$$U_l = q_l(K_l - CC_l) = \hat{U}_l - q_l(CC_l), \quad (3)$$

where $\hat{U}_l$ is the CPUE of legal slipper lobster at the preexploited stock size. By using ordinary least squares on equation (3), $\hat{U}_l$ and q_l can be estimated. Given that $\hat{U}_l = q_lK_l$, then K_l is estimated by dividing $\hat{U}_l$ by q_l.

Figure 2.—Area of intensive slipper lobster fishing by a commercial lobster vessel on Laysan bank, Hawaii.



Results

Effort was concentrated in the northwest corner of Laysan bank but extended south to a sharp drop-off along the southern portion of the bank (Fig. 2). Normally the vessel set seven strings in the northwest corner at 30-200 m, but for a brief time (5 days), two strings (320 traps) were moved from the area to explore other potential fishing sites. Catches in these traps were poor and predominantly composed of spiny lobster, which were returned to the water; therefore, these traps and catches were eliminated from the totals. Catches along the northwest corner of the bank were almost all slipper lobster. About 126,000 total slipper lobster (all categories combined) were landed from 36,000 trap-hauls, yielding an overall CPUE of 2.34 legal (retained) and 3.487 total slipper lobster per trap-haul (Table 1).

The CPUE data for legal slipper lobster were fit to the Leslie model (Ricker, 1975). The CPUE was calculated on a catch per trap-haul basis and regressed against the adjusted cumulative catch (Fig. 3), which was the cumulative catch at the start of a fishing day plus half of the catch taken during that day (von Geldern, 1961). The slope of the predicted line

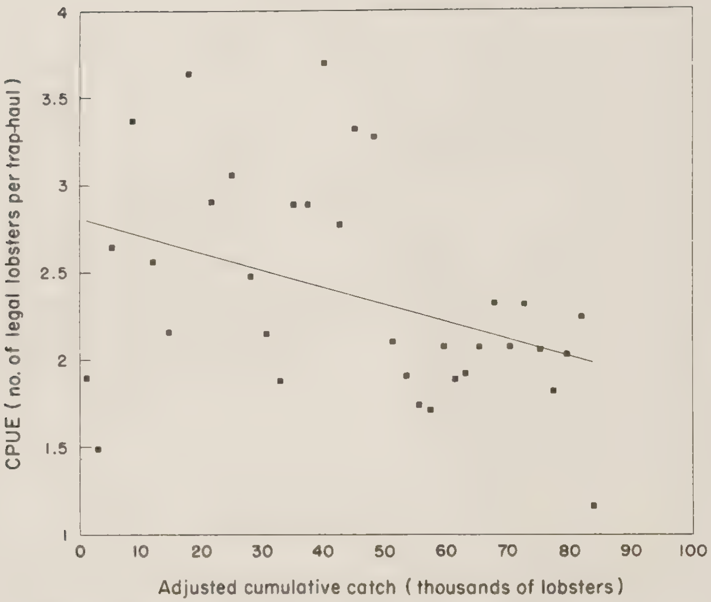


Figure 3.—Leslie model applied to the intensive fishing experiment for slipper lobster at Laysan bank, Hawaii. Each point represents 1 day of fishing. Data are from Table 1.

depicted in Figure 3 was significantly less than zero (one-tailed t-test, $P = 0.01$; $t = -2.45$; df = 32); however, the Durbin-Watson statistic (1.12) indicated autocorrelation problems, which could bias parameter estimates. By applying the Cochrane-Orcutt procedure (Wittink, 1988), the problem was corrected (DW = 2.04); the slope of the corrected line was significantly less than zero (one-tailed t-test, $P = 0.05$; $t = -2.25$; df = 32). The slope of the corrected line is -1.52×10^{-5} (SD = 6.76×10^{-6}), and the y-intercept is 3.10 (SD = 0.204). Therefore, the catchability coefficient is an estimated 1.52×10^{-5} trap-haul^{-1}, and the initial stock size is 204,000 slipper lobster with tails of 85 g or greater [confidence intervals: $P(7.49 \times 10^{-6} < q < 1.22 \times 10^{-5}) = 0.95$ and $P(181{,}945 < K < 970{,}786 = 0.95$, respectively]. An estimate of CPUE at virgin biomass is 3.10 [confidence interval: $P(2.68 < u_K < 2.94) = 0.95$].

As suggested by several previous investigators, the possibility of heteroscedasticity in the plot of CPUE against adjusted cumulative catch was explored by using the Goldfeld-Quandt test in Wittink (1988). A regression of CPUE on adjusted cumulative catch revealed that the sample variance (S) for the first 14 fishing days ($S^2{}_1 = 0.417$) and the last 14 fishing days ($S^2{}_2 = 0.105$) indicated no evidence of heteroscedasticity ($S^2{}_2/S^2{}_1 < F_{12,12}$ at 0.05). In addition, a runs test on the signs of the residuals indicated they were randomly sequenced ($P > 0.50$). The effects of the lunar cycle were tested by using a dummy variable and found not to be statistically significant ($P = 0.05$).

Discussion and Extrapolation of Results

The commercial data presented appear to give reasonable results; however, initially it may be appropriate to consider whether any of the basic assumptions of the Leslie model were violated. The initial assumption of an isolated population is evident by the geographical features of Laysan bank, which rises out of several thousand meters of water. Although the recruitment pattern of spiny lobster larvae in the NWHI is believed to be regionwide (MacDonald, 1986), there is no evidence to support postsettlement migration between banks by any species of lobster. Bathymetric charts of the fishing area show a sharp drop-off on the southwestern corner of the bank that may act as an additional physical barrier to substantial immigration to or emigration from other parts of the bank during the fishing period. Anecdotal information from experienced lobster fishermen indicates that steep drop-off areas are not normally conducive to large concentrations of lobster, but slipper lobster may be present. The northern extent of trapping does not show as good a physical boundary as in the south, but no trap strings were fished east of lat. 171°45′W, except those eliminated as exploratory. Therefore, we believe our initial assumption was fulfilled during the experiment.

The second assumption that changes in population stock size were due only to fishing mortality is more difficult to prove, though there is little evidence to the contrary. The fishing period was relatively short; however, one cannot rule out the possibility that recruitment to the fishery may have occurred or that mortality was abnormal. Little information presently exists on the molting and recruitment patterns of slipper lobster. The time from their settlement as pueruli to recruitment to the fishery is estimated at 3.3 years (Polovina and Moffitt[5]), of which the 34-day fishing period represents a small (2.8 percent) proportion. No data exist on the proportion of the population undergoing molting, which may alter their foraging behavior and thus the probability of capture by baited traps. In other lobster species, these changes can cause corresponding changes in the catchability coefficients (Morgan, 1974; Newman and Pollock, 1974). Our data

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[5] Polovina, J. J., and R. B. Moffitt. 1989. Status of lobster stocks in the Northwestern Hawaiian Islands, 1988. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-89-3, 10 p.

Table 2.—Estimated total catch per unit effort (CPUE; number of lobster per trap-haul) and stock size of slipper lobster in the lobster fishery in the Northwestern Hawaiian Islands, 1985-86[1]. NF = no fishing.

Location	CPUE 1985	CPUE 1986	Area[2] (km^2)	Stock (No.) 1985	Stock (No.) 1986
Nihoa	NF	1.04	124.8		17,708
Necker Island	0.83	0.40	1,913.2	216,654	104,412
French Frigate Shoals	0.41	0.39	538.8	30,140	28,670
Brooks Banks	1.84	1.50	406.2	101,973	83,130
St. Rogatien	0.91	0.66	476.4	59,148	42,899
Gardner Pinnacles	1.46	0.56	3,000.4	597,670	229,243
Raita	0.52	0.73	697.9	49,514	69,510
Maro Reef	1.63	1.04	1,887.6	419,785	267,838
Pearl and Hermes Reef	0.75	NF	426.7	43,663	
Kure Atoll	0.48	NF	66.0	4,323	
Lisianski Island	0.66	1.77	922.2	83,042	222,704
Midway	0.35	NF	268.4	12,817	
Other[3]		2.47	1,947.0		656,133
Total				1,618,729	1,722,247

[1] Clarke, R. P., S. G. Pooley, P. A. Milone, and H. E. Witham. 1988. Annual report of the 1987 western Pacific lobster fishery. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-88-5, 48 p.

[2] From text footnote 2.

[3] Includes Northampton Seamount, Pioneer Bank, Pearl and Hermes Reef, Midway, Kure Atoll, an unnamed bank north of St. Rogatien, and Laysan bank.

and statistical analysis indicate that q, the catchability coefficient, was constant during the exploitation at Laysan bank. Without any evidence to the contrary, we believe that the third assumption (i.e., catchability was constant) has not been violated. It would have been useful for the vessel to have returned later to the bank and fished the area again to determine whether the slipper lobster CPUE stayed depressed, but this did not occur. In addition, no length-frequency information was taken, so conclusions as to shifts in size classes cannot be made.

The fact that the data had to be corrected for autocorrelation can be explained by the fishing patterns of the vessel. While the strings were moved each day, the success on any one day clearly had an effect on where the traps were set the following day, and as CPUE levels dropped, the vessel changed its pattern of fishing altogether. Daily plots of trap string locations reveal the vessel initially fished perpendicular to the depth contours of the bank, but as CPUE dropped, the vessel apparently began to set strings parallel to the depth contours at 60-120 m to better target optimal fishing areas.

Many studies using intensive fishing experiments do so with the intent of determining absolute estimates of stock size over a given unit of area (square kilometer of habitat or linear kilometer of appropriate depth contour; Polovina, 1986; Ralston, 1986; von Geldern, 1961). The same exercise was attempted for the NWHI slipper lobster population, revealing surprising results. Lobster density determined on the west and northwest portion of Laysan bank was taken as a minimum estimate of unexploited stock size for the entire bank. We believe it is inappropriate to extrapolate this density over the entire area of the bank, given the reportedly poor catches for the exploratory strings set on the other side of the bank. The NMFS lobster assessment research data from 1985 and 1986 (NMFS unpubl. data) confirm that catch rates for slipper lobster by black plastic traps were greatest in the northwest corner of the bank and diminished substantially toward the southeast portion. Therefore, for this exercise, we have applied the absolute abundance in the area fished to the entire bank.

Assuming the density estimate from Laysan bank (K/482.2 km^2) is an appropriate indicator of the potential number per square kilometer (422 slipper lobster/km^2 at the 20-200 m depths), the entire NWHI (8,876 km^2 of potential habitat at the 20-200 m depths) would have 3.75 million legal slipper lobster. Previous estimates of K for the entire NWHI equaled 3-4 million legal spiny and slipper lobsters combined (Polovina, 1989). Fishery catch totals for spiny lobster were equal to or greater than those of slipper lobster during 1985-88. This method of assuming an even distribution of slipper lobster over the entire potential area yields results that are twice the previous estimates. Slipper lobster at Laysan bank apparently were concentrated on the northwest corner of Laysan bank for some unknown reason, and an alternative method of extrapolation was necessary to account for this patchiness.

The alternative method assumes that slipper lobster distribution varies from bank to bank in the NWHI. The only measure of relative abundance for all the banks fished is from commercial catch and effort data collected during the initial years (1985-86) of slipper lobster exploitation; however, as will be discussed later, these data have limitations also. The estimate of catchability coefficient for Laysan bank was applied to obtain bank-specific densities for those areas reported as being fished. These values were multiplied by the bank's horizontal planar area relative to Laysan bank (Table 2). The CPUE data represent total slipper lobster caught; therefore, the estimates were adjusted by the same factor as that seen at Laysan bank to exclude sublegal and berried lobster.

The resulting estimates of stock size appear questionable even when adjusted for catches of sublegal and berried slipper lobster. In the NWHI, a total of 1.19 million slipper lobster were reported caught in 1985 and 1.24 million in 1986. Adjusting these catches by eliminating the sublegal and berried lobster shows that 74 percent (797,194 legal slipper lobster) of the estimated stock were landed in 1985 and 72 percent (829,143 legal slipper lobsters) in 1986. The value of K is underestimated by this method, because CPUE values are reported without targeting information and represent a composite of the fishing effort for spiny and slipper lobsters. Information on the targeting practices of the fishermen is not available; therefore, effort segregation is impossible.

The data show that after day 13 of in-

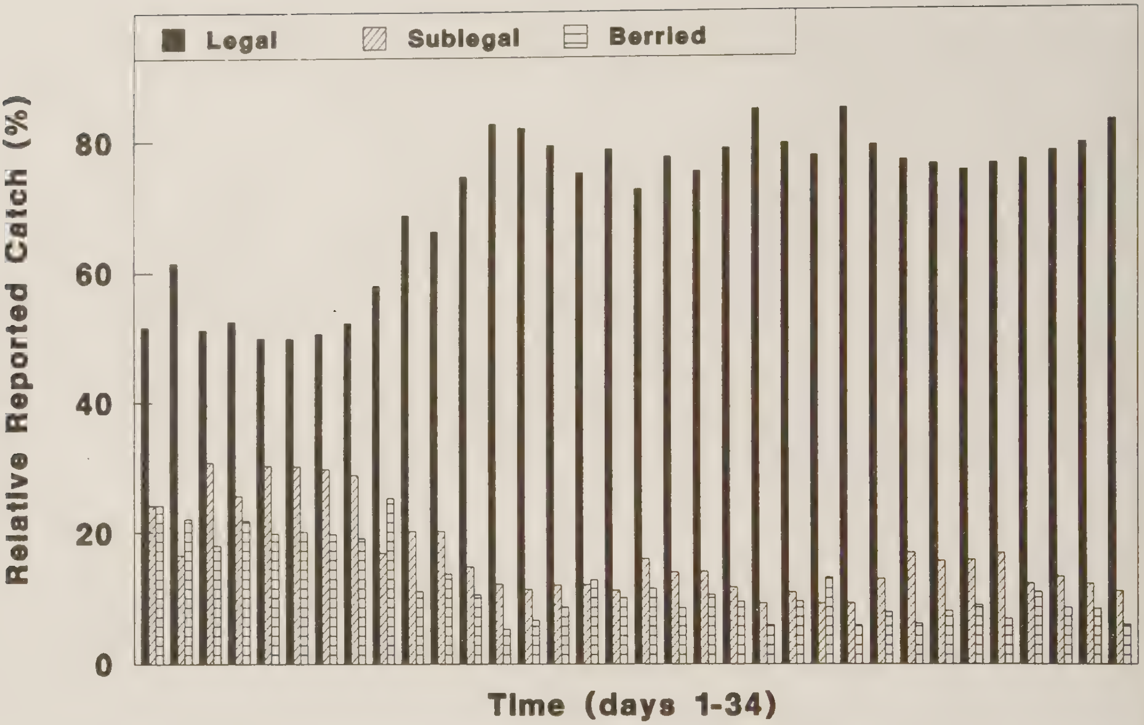

Figure 4.—Relative breakdown of reported catch categories (legal lobster have tails ⩾85 g, sublegals have tails <85 g, and berried are egg-bearing females) at Laysan bank, Hawaii, 1986.

tensive fishing at Laysan bank, the relative proportion of legal, sublegal, and berried slipper lobster stabilized (Fig. 4). Prior to that period, the percentages of berried and sublegal lobster were greater, indicating that berried females may have been releasing their eggs and becoming part of the retainable (legal) pool of lobster. However, the same trend is seen for sublegal lobster. This potential problem was cleared up in discussions with the skipper of the vessel, who indicated that numbers of berried and sublegal lobster were to be taken as estimates only and reflected estimating errors during the initial period of fishing, which was heavy even by commercial standards. As the slipper lobster CPUE declined, fishing returned to levels normally experienced by the vessel and allowed time to better estimate the numbers of sublegal and berried lobster returned to the water.

Conclusion

The use of the commercial data appears not to substantially violate any of the underlying assumptions of the Leslie model. The commercial catch data from Laysan bank produce reasonable estimates of K and q, but fishery-wide extrapolations yield estimates that are different than those presently accepted. Our results indicate that present estimates of K are probably low, and the true value probably lies somewhere between the two estimates presented here. Using two accepted methods of extrapolation, the low estimate for slipper lobster unexploited abundance is 1.2×10^6 legal slipper lobster, and the high is 3.8×10^6, yielding a mean of 2.5×10^6.

The catch data indicate that slipper lobster are extremely vulnerable to trapping, especially when concentrated in the proportions seen at Laysan bank. Catch and effort logs show fishermen have the ability to effectively target slipper lobster. Research directed at the causes of these concentrations is necessary, and if they are found to be related to some biological or behavioral phenomena and if present regulations are unable to sustain sufficient spawning stock biomass, a seasonal closure may be warranted for the slipper lobster fishery in the NWHI.

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Literature Cited

Crittenden, R. N. 1983. An evaluation of the Leslie-DeLury method and a weighted method for estimating the size of a closed population. Fish. Res. (Amst.) 2:149-158.

DeLury, M. D. 1947. On the estimate of biological populations. Biometrics 3:145-167.

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8:94-113.

MacDonald, C. D. 1986. Recruitment of the puerulus of the spiny lobster, *Panulirus marginatus* in Hawaii. Can. J. Fish. Aquat. Sci. 43: 2118-2125.

Morgan, G. R. 1974. Aspects of the population dynamics of the Western rock lobster *Panulirus cygnus* George. II. Seasonal changes in the catchability coefficient. Aust. J. Mar. Freshwater Res. 25:249-259.

Newman, G. G., and D. E. Pollock. 1974. Biological cycles, maturity and availability of rock lobster *Jasus lalandii* on two South African fishing grounds. Union S. Afr. Sea Fish. Branch, Invest. Rep. 107:1-16.

Polovina, J. J. 1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Fish. Bull. 84:423-428.

Polovina, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46:660-665.

Ralston, S. 1986. An intensive experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago. Fish. Bull. 84:927-934.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Schnute, J. 1983. A new approach to estimating populations by the removal method. Can. J. Fish. Aquat. Sci. 40:2153-2169.

von Geldern, C. E., Jr. 1961. Application of the DeLury method in determining the angler harvest of stocked catchable-sized trout. Trans. Am. Fish. Soc. 90:259-263.

Williams, A. B. 1986. Lobsters—identification, world distribution, and U.S. trade. Mar. Fish. Rev. 48(2):1-36.

Wittink, D. R. 1988. The application of regression analysis. Allyn and Bacon, Boston, 324 p.

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Biology and description of a bythitid fish from deep-sea thermal vents in the tropical eastern Pacific

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(*Received* 1 *March* 1989; *in revised form* 1 *August* 1989; *accepted* 11 *September* 1989)

Abstract—A new fish species of the world-wide genus *Bythites* (Bythitidae, Ophidiiformes) is based on a gravid female captured in a thermal vent in the Galapagos Rift Zone. No apparent morphological features of adults or larvae account for life in the vent environment. Gill arch structure does not indicate filter feeding. The few fish species living in vents are not representative of ancient groups and are probably recent arrivals. The species is intermediate between the nominal genera *Bythites* and *Abythites*; hence, the latter is considered a junior synonym. The new species differs from its four congeners in its high dorsal, anal, and pectoral fin ray counts and its broad interorbital space. Free sperm and spermozeugmata are present throughout the ovarian tissue. Intra-ovarian larvae have a well-developed yolk sac, large oil globule, and pigmented eyes. Brood size is about 10,000.

INTRODUCTION

THE earliest observers (CORLISS *et al.*, 1979) of the remarkable biota of deep-sea thermal vent systems in the tropical eastern Pacific remarked on the presence of fishes living in and around the vents. Of the approximately 20 species comprising the ichthyofauna of the general area of the Galapagos rise thermal vents (COHEN and HAEDRICH, 1983), only two have been observed living in warm water and only one is possibly an obligatory vent inhabitant (HESSLER and SMITHEY, 1984). This latter fish was identified from photographs and observations from the submersible *Alvin* as belonging to the live-bearing ophidiiform family Bythitidae and tentatively (and incorrectly) assigned to the genus *Diplacanthopoma* (COHEN and HAEDRICH, 1983; COHEN *et al.*, 1985). Similar fishes have been observed from *Alvin* and *Cyana* at vents near 11°N and 13°N (ROSENBLATT and COHEN, 1986; GEISTDOERFER, 1988).

A gravid female bythitid has now been captured from one of the Galapagos rise vents. The purpose of this paper is to discuss the classification of the species, to describe and name it, to describe what can be surmised of its reproductive biology, and to summarize what is known of the species' natural history.

SYSTEMATICS

Genus Bythites

Diagnosis. Bythitine fishes (COHEN and NIELSEN, 1978) are defined by the following combination of characters. Anal fin originating on posterior half of body, tail not greatly

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attenuate; ventral fins present, one ray in each, originating well posterior to the symphysis of the cleithra; caudal fin rays 10–13; pectoral fin rays 22–37, fin not on an elongate peduncle, pectoral radials not greatly elongate; imbricate scales present on body; no series of large circumorbital pores or prominent median interorbital pore; no prominent skin flap above opercle; opercular spine present; branchiostegal rays seven or eight; developed rakers on first gill arch 0–3; palatine teeth present; vomerine teeth not nearly or completely divided into two patches; precaudal vertebrae 13–20; male with a stalked intromittent organ.

Discussion. Although *Bythites* was first named in 1835, fishes of the genus are rare in collections. In a review published in 1973, Nielsen and Cohen recognized three North Atlantic species, *B. fuscus* Reinhardt, still known only from the holotype, and *B. islandicus* and *B. gerdae* which they described based on four and two specimens, respectively. In the same paper they proposed the genus *Abythites* for the western Pacific *B. lepidogenys* Smith and Radcliffe (with *B. matsubarai* Arai as a junior synonym).

The nominal genera *Bythites* and *Abythites* were separated by six characters (NIELSEN and COHEN, 1973). The fish described below as *Bythites hollisi* agrees with *Bythites* in three characters, with *Abythites* in two, and is intermediate in one (Table 1). Several alternate courses of action to resolve the issue of appropriate generic placement for *B. hollisi* are possible. These include the assignment of *B. hollisi* to a monotypic genus, inclusion of *B. hollisi* as a fourth species of *Bythites* or a second species of *Abythites*, or the placement of *B. hollisi* in an expanded genus *Bythites* with *Abythites* as a synonym.

B. hollisi is readily distinguishable from any of the three species of *Bythites* and the single species of *Abythites* (Table 2) in having more fin rays and vertebrae and a relatively broader inter-orbital and smaller eye (the two proportional characters are due perhaps to allometric growth, as the type of *B. hollisi* is more than twice as long as the next largest specimen of *Bythites*, the type of *B. fuscus*). There seem to be no other unique character states, however, distinguishing *B. hollisi.* Considering how little is known of the characters listed in Table 1, it is difficult to justify assigning *B. hollisi* to one or the other genus or to erect yet another monotypic genus.

Recognizing an expanded *Bythites* including *fuscus*, *islandicus*, *gerdae*, *lepidogenys* and *hollisi* creates a taxon that can be diagnosed only on the basis of a combination of character states (presented above as the diagnosis), many of which are probably plesiomorphic; there are no known synapomorphies for the five species combined. However, the alternative of erecting five monotypic genera would not clarify relationships and would burden the literature with still more names. Pending a more thorough study of bythitid genera and assessment of characters, the most practical, if not particularly satisfying, course of action is to recognize a possible paraphyletic *Bythites* containing five species.

Table 1. Character states in the nominal Genera Bythites, Abythites *and in* B. hollisi

	Bythites	*Abythites*	*B. hollisi*
Scales on head	Absent	Present	Absent
Tooth shape	Needle-like	Granular	Needle-like
Pseudobranch filaments	0	2	1
Developed gill rakers on anterior gill arch	0–1	3	3
Shape of precaudal neural spines nos 5–9	Pointed	Blunt	Pointed
Ribs on precaudal centra nos 1 and 2	Yes	No	No

Table 2. Comparison of characters in five species of Bythites. *Data from* Arai (1969) *and* Nielsen *and* Cohen (1973)

	B. hollisi	*B. fuscus*	*B. islandicus*	*B. gerdae*	*B. lepidogenys*
N	1	1	4	2	2
Standard length (SL)	304	146	72–88	59–63	72–99
Anal fin rays	88	70	46–50	51–56	49–56
Dorsal fin rays	122	88	76–79	87–94	75–81
Pectoral fin rays	37	29–30	25–26	24–27	22–24
Developed rakers on anterior gill arch	3	0	0	1	3
Form of small gill rakers	Separate knobs	Separate knobs	Separate knobs	Plate-like and coalesced	Separate knobs
Anterior anal fin ray below dorsal fin ray no.	41	27	29–32	43–44	24–29
Total vertebrae	76	53	40–50	46–47	44–45
Fleshy interorbital as % of SL	10.7	8.9	8.0–9.0	6.7	7.0–8.3
Diameter of eye as % of SL	3.0	4.8	5.5–6.0	4.8–5.0	3.9–4.9
Pairs of large pores on lower jaw	2	2	2	5	5
Branchiostegal rays	8	7	7	8	8

Table 3. Areal and depth distribution of five species of Bythites. *Data from* ARAI (1969) *and* NIELSEN *and* COHEN (1973)

	Area	Depth (m)
B. fuscus	West Greenland	"From great depths"
B. gerdae	Straits of Florida	786–832
B. hollisi	Galapagos thermal vent area on east Pacific rise	2500
B. islandicus	Southeast Iceland	229–283
B. lepidogenys	Philippines	296–400
	Tosa and Suruga Bays, Japan	100–400

Relationships. Among the dozen or more presently recognized genera (many of which are poorly defined) of the subfamily Bythitinae, *Bythites* is perhaps most similar to *Saccogaster*, which is characterized by having reduced body squamation and elongate pectoral radials. The former character is reductional and the latter needs closer investigation in *Bythites* than is possible with available material.

Species and distribution. The species are diagnosed in Table 2 and their known distributions are summarized in Table 3.

Bythites hollisi n. sp.

Brotulid fish; CORLISS and BALLARD (1977; color illustration).

Ophidioid fish; CORLISS *et al.* (1979).

"Vent fish" (a bythitid); LUTZ and HESSLER (1983) (color illustration from Corliss and Ballard).

?*Diplacanthopoma* (vent fish); COHEN and HAEDRICH (1983).

?*Diplacanthopoma*; HESSLER and SMITHEY (1984) (Fig. 5, color, Fig. 7).

(Un-named fish); JANNASCH (1984) (Fig. 1, color).

?*Diplacanthopoma* sp. (vent fish); COHEN *et al.* (1985).

Possibly *Diplacanthopoma*; GRASSLE (1985).

Diplacanthopoma; ROSENBLATT and COHEN (1986).

Diplacanthopoma (?); GEISTDOERFER (1988).

Bythites; HESSLER *et al.* (1988).

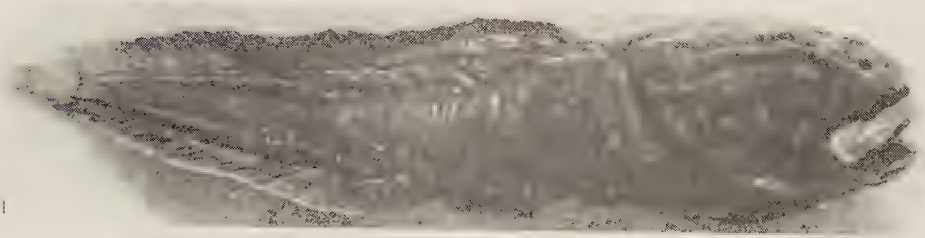
Diagnosis. See Table 2.

Holotype. SIO 88–97, a gravid ♀ 304 mm SL. Hydrothermal vent (Mussel Bed) on the Galapagos Rift Zone, 0°47.894′N, 86°9.210′W, 2500 m, D.S.R.V. *Alvin* dive 2026, 28 April 1988, R. Hollis, R. Hessler and J. O'Brien. Taken in a net held by the manipulator arm.

Etymology. Named for expert *Alvin* pilot Ralph Hollis, who finally captured this elusive fish.

Counts. Dorsal fin rays 122, anal fin rays 88, pectoral fin rays 37, ventral fin ray 1, caudal fin rays 12, branchiostegal rays 8, developed gill rakers on first arch 3, vertebrae (not counting ural centra) 20 + 56 = 76, first dorsal fin ray above approximately centrum 11, 1st anal fin ray below approximately centrum 29, first anal fin ray below approximately dorsal ray 41.

Measurements. (Some data imprecise due to partial mutilation of the specimen when tissue was dissected for physiological and biochemical analyses.) mm followed by percent SL in parentheses: SL 304; head length 92 (30.3); snout length 20.6 (6.8); upper jaw length 43.6 (14.3); horizontal eye diameter 9.2 (3.0); fleshy interorbital width 32.5 (10.7);



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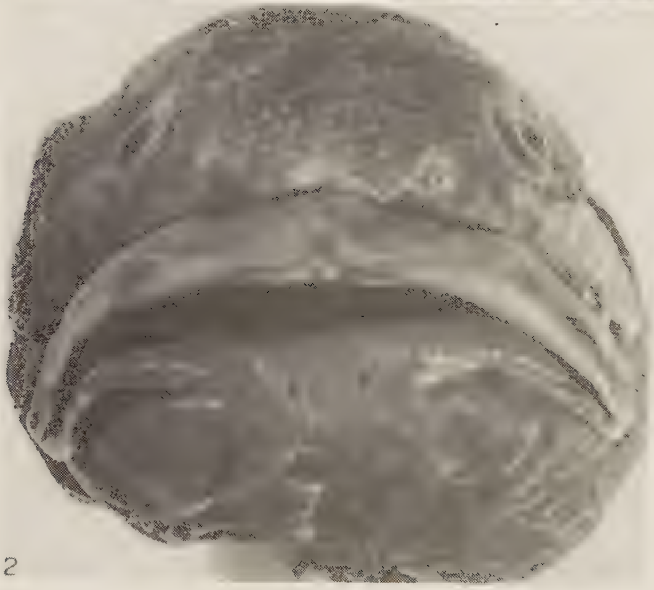

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Fig. 1. *Bythites hollisi*, holotype, SIO 88–97, SL 304 mm.

Fig. 2. *Bythites hollisi*, holotype, SIO 88–97, SL 304 mm, anterior view.

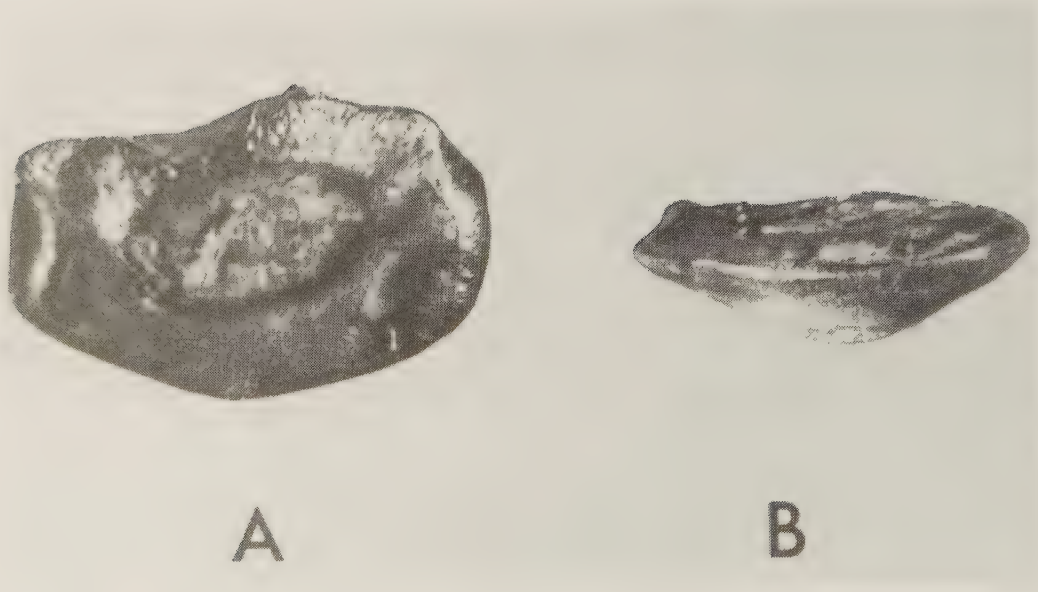

Fig. 4. *Bythites hollisi*, holotype, SIO 88–97, left sagitta, length 7.8 mm. (A) Medial view; (B) ventral oblique view.

body depth at vent 41.5 (13.7); preanal length 168 (55.3); predorsal length (measured from an X-ray photograph) 115 (37.8); least depth pectoral fin base 23.1 (7.6); pectoral fin length 36.2/41.4 (11.9/13.6); ventral fin length 20.5 (6.7).

Description. Body compressed, depth at vent about 7.3 in SL; tail not greatly attenuate (Fig. 1).

Head (Fig. 2) 3.3 in SL, depressed, slightly broader than deep; snout blunt, slightly rounded in lateral view, broadly rounded from the dorsal aspect. Anterior nostril a small pore with a slightly raised rim, located above the upper lip slightly medial to the level of the dorsal margin of the eye; posterior nostril a small, rimless pore located anterior to the midlevel of the orbit about mid-way between the anterior nostril and the anterior margin of the eye. Eye small, 2.2 times in snout length, 10 times in head length; in preserved holotype covered with a translucent spectacle. Jaws subequal; thick and fleshy; upper jaw oblique, extending posteriorly more than an eye diameter beyond the level of the posterior margin of the eye; maxillary probably sheathed posteriorly when the mouth is closed; rear margin with a slight concavity, neither rounded nor greatly expanded; no posterior-ventral spine or point. A single short, strong and blunt spine on the opercle, buried but visible inside the gill chamber.

The dorsal fin originates above the mid-length of the pectoral fin; the anal fin originates posterior to the mid-length of the fish. The pectoral fin is a broadly rounded paddle on a peduncle that is more than twice as deep as it is long; fin membrane frayed distally, rays unbranched, their tips free and filamentous. The ventral fins are closely adjacent at their bases, and insert well posterior to the symphysis of the cleithra (about 25 mm, although measurement is imprecise due to mutilation of the specimen). The caudal fin is confluent with dorsal and anal fins, posteriorly rounded, its rays not exserted. The dorsal-most caudal ray is apparently supported by an epural, 10 rays insert on posterior hypurals, and the ventral-most caudal ray is supported by a process (? parhypural or hypural) on PU1 or PU1 + U1.

The skin is thick and tough. Color in alcohol a dingy dark gray, paler posteriorly; lips pale; series of small papillae on the head are indicated by small, oval to elongate pale areas which are most densely distributed on the snout (see below). The broadest parts of the head (which is the broadest part of the fish) has many randomly arrayed pale narrow streaks which may represent scars. Tiny imbricate scales cover the entire body and extend far anteriorly on the occiput; the fins and the head are naked. Minute, dark papillae, embedded in congealed mucus in most areas, are evenly distributed on the head. Larger white papillae are arrayed in generally linear series on the post-orbital region of the head and are more densely distributed in an apparently random pattern on the snout and chin. A series of about 60 similar surface (although mostly embedded in mucus) white papillae marks the course of the lateral line along the body, originating anteriorly at the upper angle of the gill opening, descending gradually to the mid-line at about the level of the vent, and then coursing posteriorly and becoming obscure at nearly the end of the body; the anterior lateral line papillae arise from the surface of the skin; more posteriorly they arise from the anterior margin of small, anteriorly directed pits.

Mandibular pores 2; the most anterior is directed forward at the tip of the lower jaw; the other is immediately posterior in the gular fold and faces posteriorly. Preopercular series with a single pore posterior to the distal end of the premaxillary and about one-half the distance from that point to the level of the rear margin of the head. Supraorbital series with a single pore medial to the anterior nostril. Infra-orbital series with two pores in the skin fold over the upper lip ventral to the space between the two nostrils. No lateral or supratemporal pores.

Premaxillary teeth tiny, conical, sharply pointed, in a narrow band that is about 4–5 teeth wide slightly posterior to the symphysis and narrows to a single tooth row posteriorly. Dentary teeth slightly larger and stouter than upper jaw teeth and in a narrower band. Vomer and palatines bear teeth that are similar to those on the dentary, in a broadly V-shaped band on the vomer and a straight, narrow band on the palatine. No median basibranchial tooth patch. Tongue broad.

The branchial arches were excised without care before we received the specimen and only those from the right side are available; the first three were dissected out, number 4 remains in place. The first arch (Fig. 3) bears three small tubercles on the upper arm, a developed raker at the angle, two developed rakers on the lower arm, with a tubercle in each interspace, and a series of at least 14 tubercles on the lateral face of the ceratobranchial following the most anterior developed raker. A series of at least 14 larger tubercles on the medial face of the lower arm interlock neatly with a series of tubercles on the lateral face of the lower arm of the second arch. A similar arrangement of interlocking tubercles is present on subsequent gill arches. The gills are well developed, with filaments reaching a length of 11 mm on the lower arm of the first arch. Arches 2 and 3 also bear well-developed filaments. (Gills have been removed from the fourth arch.) A pseudobranch consisting of a single filament is present on the left side; the corresponding area on the right side has been mutilated.

The fish has been gutted, and most of the lining of the peritoneum removed; however, it is apparently dusky; the branchial chamber is mostly pale. The tongue and floor of the mouth are pale; the roof of the mouth is light gray.

The external urogenital area consists of a prominent fleshy mound covered with fleshy papillae and compressed, leaf-like structures.

The fish is well ossified. The first neural spine is shorter than following ones; all neural spines have sharp points. Ribs are lacking on centra 1 and 2; vertebrae 3–6 bear ribs

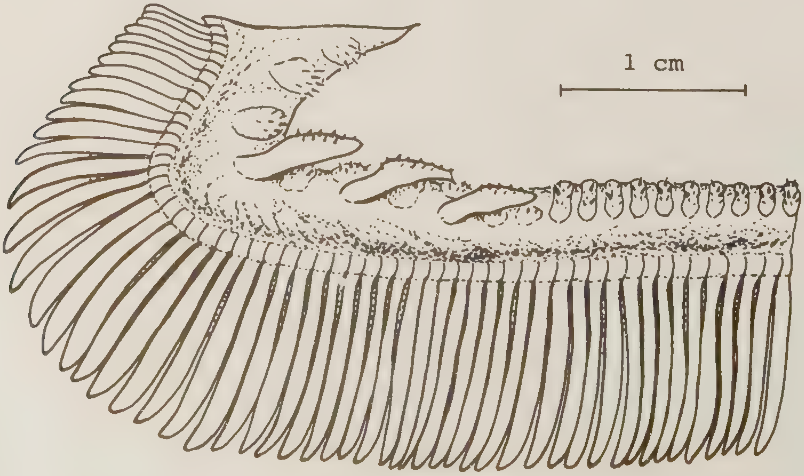

Fig. 3. *Bythites hollisi*, holotype, SIO 88–97, lateral view of first gill arch.

directly on the centra; 7–15 have ribs at the ends of progressively longer parapophyses; ribs on vertebrae 7–14 bear slender epipleurals.

The sacculith (sagitta) is 7.8 mm long, 5.0 mm in the dorso-ventral dimension, and 2.9 mm wide. The anterior margin is broadly rounded; the dorsal margin is slightly convex anteriorly and straight posteriorly; the posterior margin is truncate; the ventral margin is a smooth curve. The medial face of the otolith is nearly flat; however, it bears the outline of a nearly oval sulcus that is 4.3 mm long and 2.1 mm deep and is closer to the dorsal margin than to the ventral one, is not divided into ostium and cauda, and has no connection with an excisura. The lateral face is a prominent dome, broadest slightly posterior to the mid-length of the sacculith. Although the form of this otolith fits well NOLF's (1980) characterization of Bythitidae and in general resembles his figures of *Abythites lepidogenys*, *Bythites fuscus* and *B. gerdae* (plate 12, Figs 1–3), it differs from all of them in its markedly truncate posterior margin.

REPRODUCTIVE BIOLOGY

The specimen is a pregnant female that extruded larvae in the transport container on the way to the surface. The ovaries were removed in the shipboard laboratory and preserved in a solution of glutaraldehyde and 10% formalin. The ovaries are paired; each consists of an elongate mass of tissue surrounded by a thin-walled ovisac. The ovisacs converge posteriorly to form a short oviduct. The left ovary is 42.9 mm long × 17.1 mm wide; the right ovary measured 46.1 × 24.2 mm. Together their blotted wet weight was 16.6 g. Each ovary has a vascular trunk along its dorsal surface with branches of the ovarian artery and vein extending into the ovigerous tissue and the ovisac (Fig. 5). The left ovary had apparently extruded most of its brood, and the right ovary appears intact.

The ovarian tissue is arranged in irregular transverse folds that protrude into the lumen formed by the ovisac (Fig. 5C). The surface of the folds consists of thin-walled vascularized sacs or bulbs of varying sizes up to about 4.0 mm in length and 2.2 mm in diameter (Fig. 5D). A mode of yolked ova about 0.2 mm in diameter (up to 0.28 mm) is visible macroscopically. The larvae lie freely in the lumen and in the crevices formed by the folds.

Histological examination of the ovarian tissue showed the highly vascularized nature of the epithelial sacs which branch from the deeper-lying ovigerous tissue (Fig. 6). This tissue contains nests of oogonia surrounded by oocytes with diameters ranging up to those mentioned above (Fig. 6B). Also scattered throughout the ovarian tissue are structures that appear to be postovulatory follicles, each with well-developed epithelial walls and nuclei concentrated towards the lumen (Fig. 6C). Atretic oocytes are encountered infrequently in the sections (Fig. 6D). The inner surface of the ovisac is covered completely with a capillary bed (Fig. 6A). Sperm are present throughout the ovarian tissue, on epithelial surfaces and interstitially. Clumps of sperm in the form of spermozeugmata appear throughout the sections, usually in crevices at the bases of the epithelial bulbs. Frequently, the clumps have penetrated the connective tissue and lie next to the largest oocytes (Fig. 6D).

The larvae are hatched, have well-developed yolk sacs containing segmented yolk, a large anteriorly placed oil globule, and lack absorptive structures such as trophotaeniae (Fig. 7). The mouth is rudimentary. Small pectoral fin buds are the only fins represented; a well-developed median finfold about half as deep as the tail extends along the entire dorsum and ventrally as far forward as the anus. The heart is differentiated enough to be functional. The eyes are formed and pigmented.

The entire brood from the right ovary was counted giving a total of 4900 larvae (exact count). The appearance of this lobe suggests that few if any larvae were lost during transit to the surface. In contrast, few larvae were present in the left lobe. Since the lobes are symmetrical, and probably contained about equal numbers of larvae, the estimated total brood size is 10,000.

Body lengths for a sample of 25 larvae ranged from 4.8 to 5.6 mm (mean = 5.1 mm ± 1.93 S.D.). A sample of 10 larvae were measured. Mean values in mm with standard deviations for seven body parts are as follows: yolk sac length, 1.1 ± 0.09; yolk sac depth, 0.72 ± 0.02; oil globule diameter, 0.56 ± 0.04; head length, 0.71 ± 0.05, body depth at pectoral fin base (not including yolk sac), 0.35 ± 0.03; snout to anus length, 2.6 ± 0.09; eye diameter, 0.28 ± 0.02. The larvae are relatively heavily pigmented with small melanophores of about equal size. These are scattered above the hindbrain and continue posteriad along the entire dorsum as two continuous rows. A single midlateral row is present on each side. A line of melanophores is present on each side above the gut and yolk sac; these extend anteriorly below the hindbrain and posteriorly as a single line along the midventral margin of the tail.

The large numbers of young, the developmental coherence of the brood and the appearance and state of development of the larvae are similar to what we know of other bythitids with pelagic young (e.g. *Brosmophycis marginata*, MOSER, unpublished observations). The question of larval recruitment is an intriguing one. If they are benthic, or benthopelagic, how do they disperse to distant vents through food-poor or otherwise unsuitable areas? If they ascend to relatively food-rich surface waters, how do they locate the specialized adult habitat?

The profusely vascularized epithelial bulbs provide a highly developed mechanism for brood maintenance as proposed by SAUREZ (1975) for similar structures found in *Ogilbia cayorum*. These are undoubtedly efficient in gas exchange, in removal of metabolic wastes, and may perform a trophic function. Other apparently ovoviviparous fishes have been shown to provide maternal nutrition (e.g. BOEHLERT and YOKLAVICH, 1983; BOEHLERT *et al.*, 1987) and it may be that no teleosts are truly "ovoviviparous." The presence of a mode of small initially yolked oocytes suggests sequential brood production. This is further supported by the abundance of sperm and spermozeugmata interspersed in the ovigerous tissue and concentrated near the larger oocytes. The presence of a mode of well-formed postovulatory follicles in an ovary containing relatively advanced young is paradoxical since these structures are typically transitory. Perhaps some development had taken place within the follicles before the young were "ovulated" into the lumen (see review of this phenomenon in bythitids by WOURMS, 1981). Alternatively these postovulatory follicles may be specialized to perform some gestational function, such as the secretion of hormones or trophic compounds.

NATURAL HISTORY

The family Bythitidae, to which *B. hollisi* is assigned, includes most of the live-bearing fishes that were formerly classified in the nominal family Brotulidae. Seventy-two species of living bythitids are listed by COHEN and NIELSEN (1978); however, there are probably a hundred or more un-named ones.

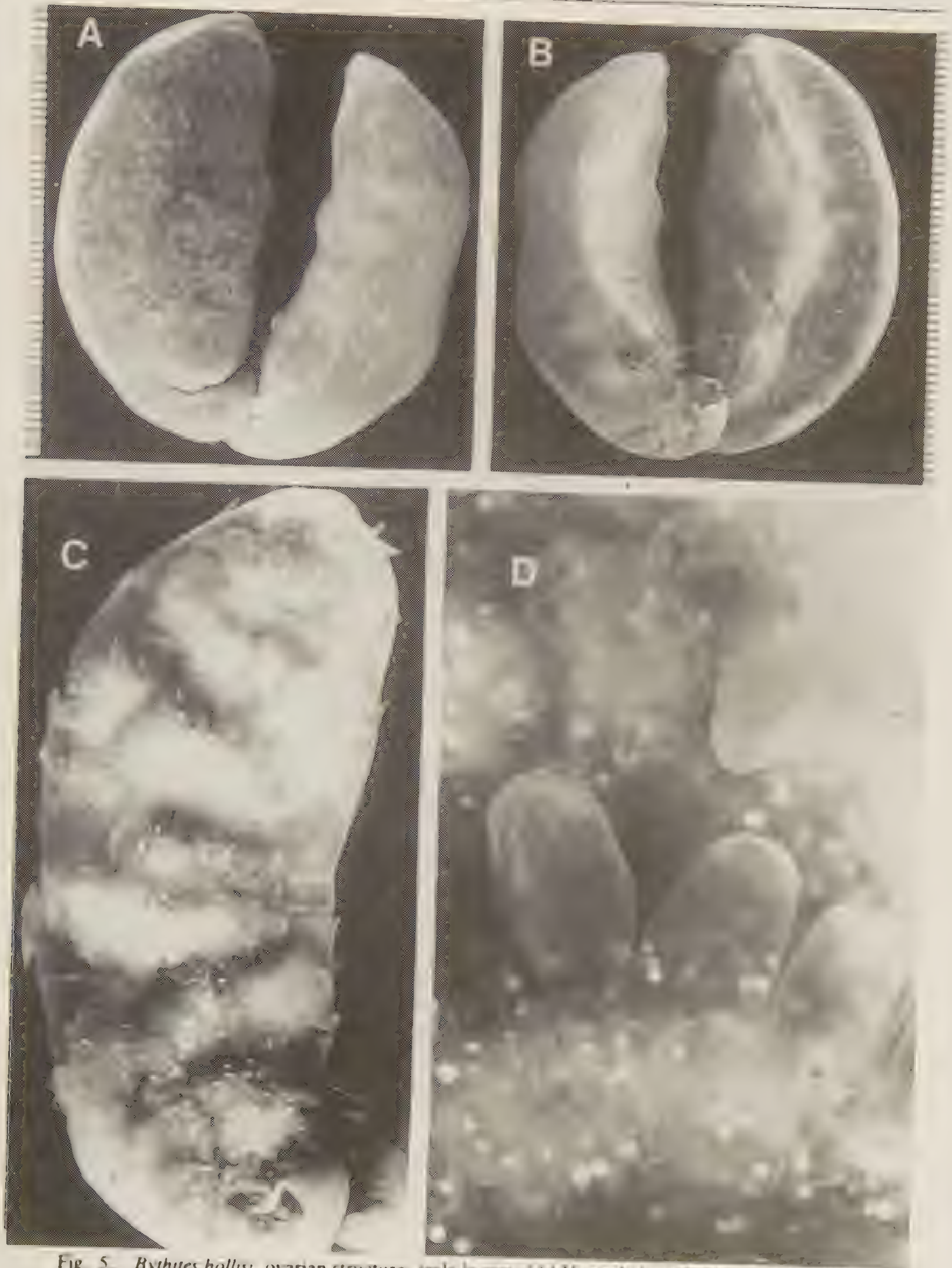

Fig. 5. *Bythites hollisi*, ovarian structure, scale in mm. (A) Ventral view of paired ovaries; (B) dorsal view showing vascular trunks and mesenteries; (C) ventral view of right ovary with ovisac and brood removed to show ovigerous tissue and epithelial bulbs; (D) enlarged view of epithelial bulbs showing their vascular networks. Note mode of small oocytes.

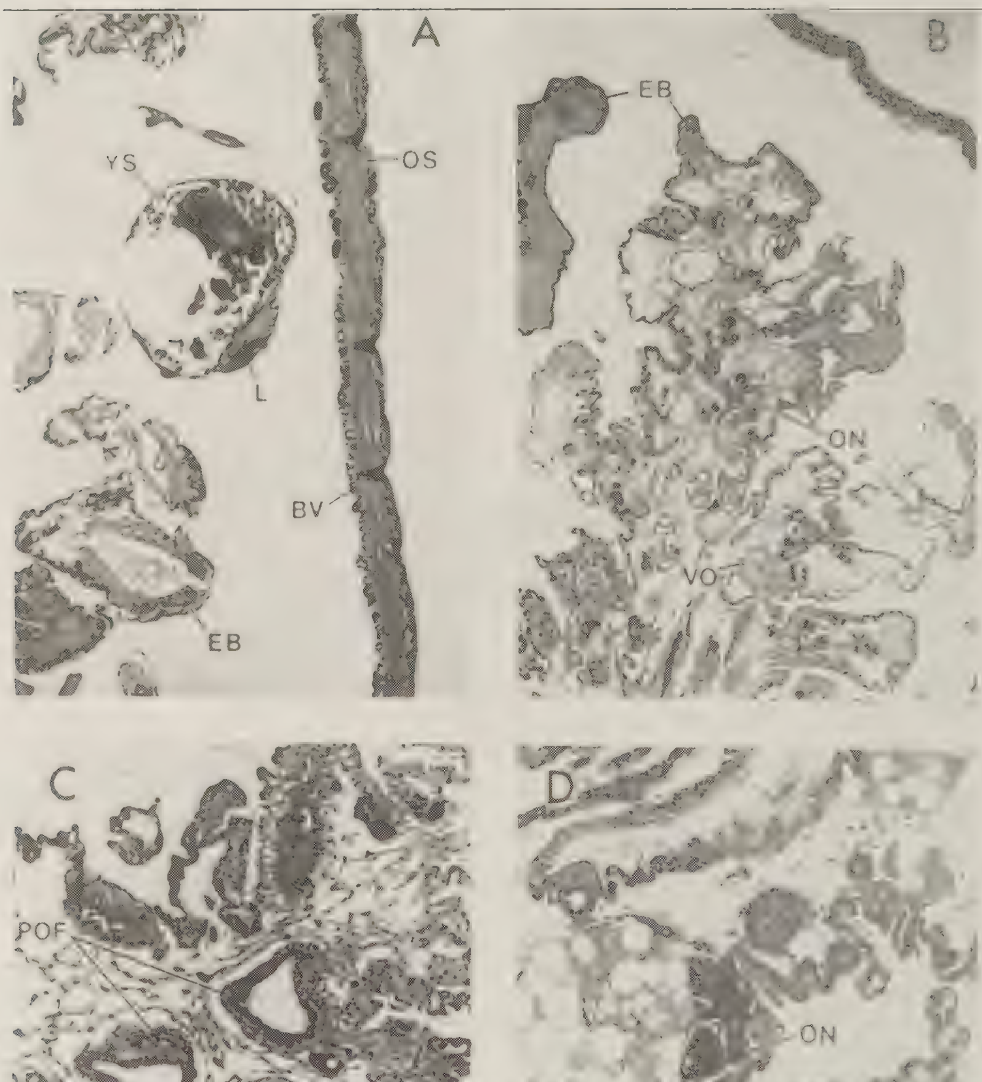

Fig. 6. *Bythites hollisi*, histological structure of the ovary. (A) Region near ovisac (OS) showing larva (L) with large yolk sac (YS), note epithelial bulbs (EB) and layer of blood vessels (BV) on inner surface of ovisac. ×25. (B) Ovigerous tissue containing oogonial nests (ON) and vitellogenic oocytes (VO), with portions of epithelial bulbs at margin. ×25. (C) Vitellogenic oocyte and two postovulatory follicles (POF). ×100. (D) Enlarged view of ovigerous tissue showing vitellogenic oocyte, oogonial nest, and atretic follicle (AF), note spermozeugmata (SZ) in contact with oocyte. ×250.

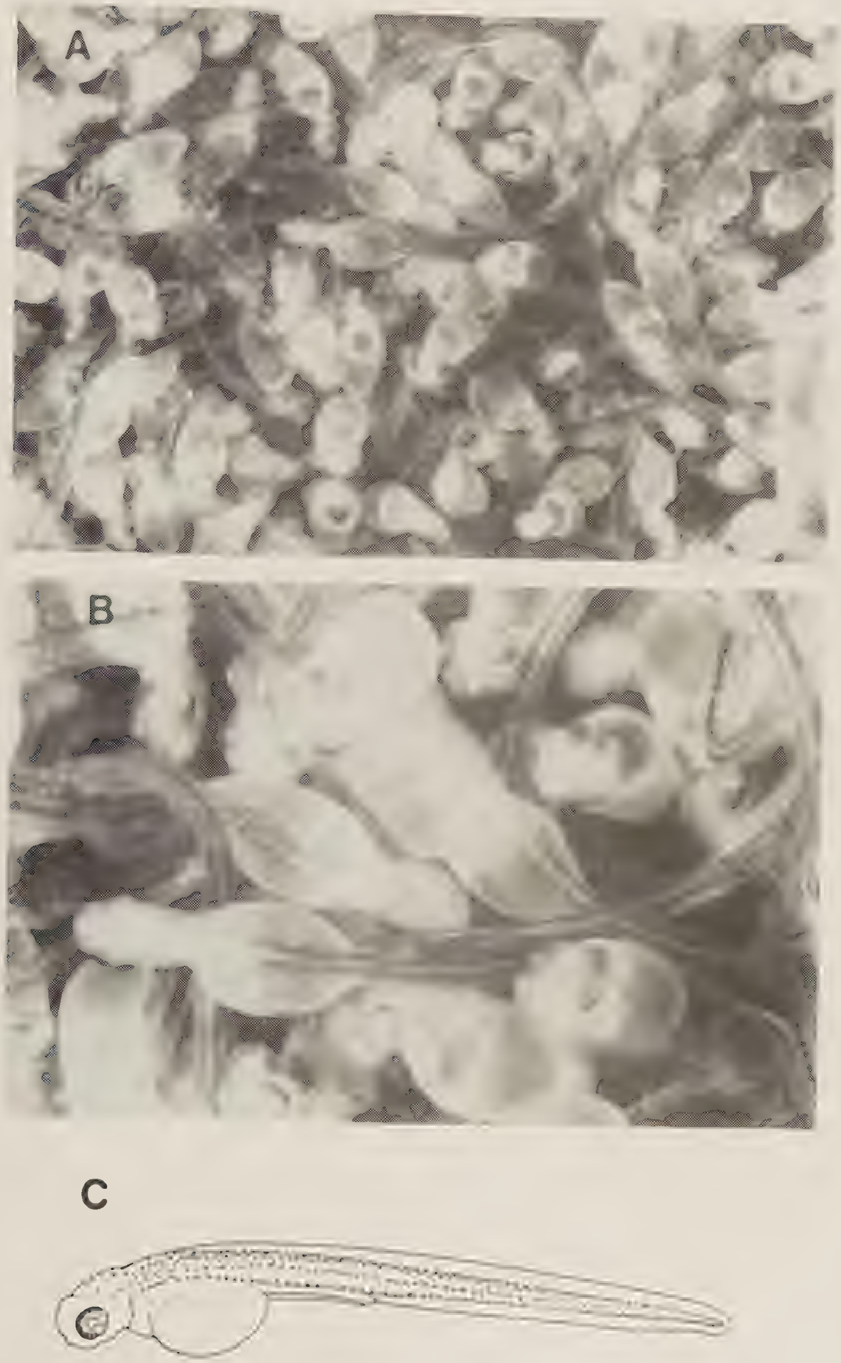

Fig. 7. *Bythites hollisi*, larvae. (A) Brood lying within ovarian lumen; (B) enlargement of portion of A; (C) drawing of yolk-sac larva, length 5.6 mm.

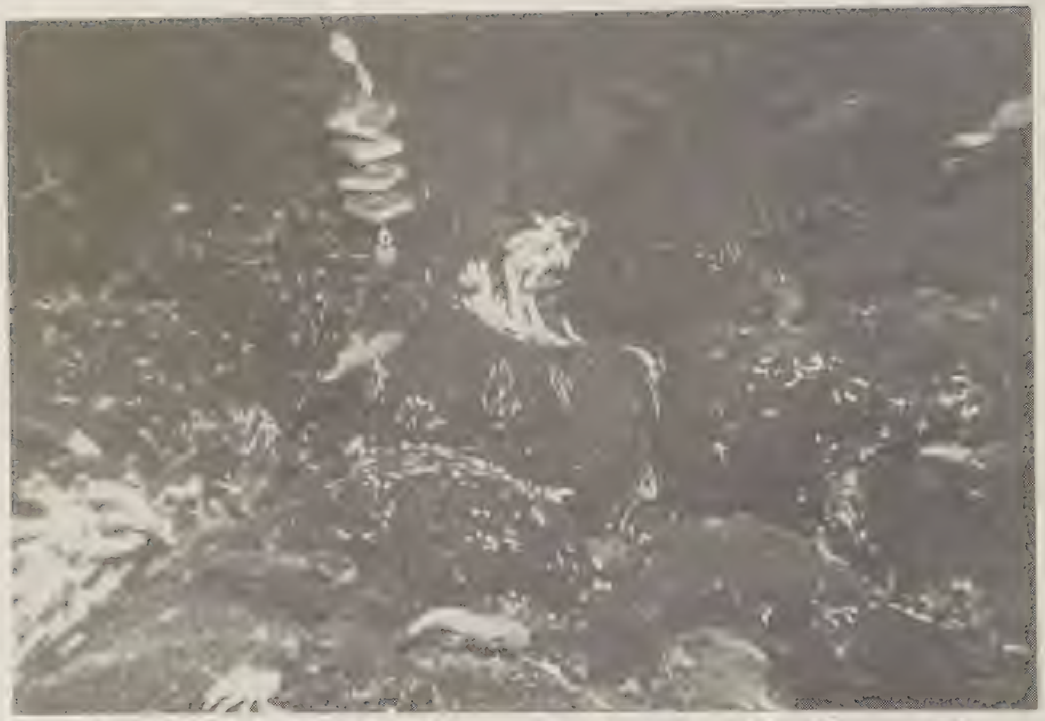

Fig. 8. *Bythites hollisi* at Garden of Eden thermal vent area. *Alvin* dive 993, 10 December 1979

Bythitids vary widely in habitat and mode of life. The greatest diversity, comprised chiefly of undescribed species, consists of cryptic tropical reef dwellers; fewer species are found in temperate shallow waters; and very few species are known to live in fresh to brackish water caves and sinkholes in the Bahamas, Cuba, Yucatan and the Galapagos Islands. The second most diverse region is on the outer shelf and mid to upper slope, where four species of *Bythites* have been taken (Table 3) and most bythitids probably are benthopelagic. Finally, at least two species are mesopelagic.

Bythitids vary also in size, ranging from species of the Indo-Pacific reef dwelling genus *Microbrotula*, which mature at less than 40 mm, to the deep-sea species *Cataetyx laticeps* which reaches 665 mm.

Living *B. hollisi* have a pink to light tan body; the head and fins are pale blue-gray; in some photographs the lips are pink; the eyes are clear and dark.

General comments on behavior based on observations from *Alvin*, still photographs, and video are given by COHEN and HAEDRICH (1983, p. 376, quoted by COHEN *et al.*, 1985) and HESSLER and SMITHEY (1984). Although *B. hollisi* has almost always been seen above or on the substrate (Fig. 8), narrow pale streaks on the postorbital part of the head (which has the greatest circumference of any part of the fish) suggest that it may at least occasionally enter narrow passages with sharp edges.

Whether the small eyes are image forming or otherwise functional is not known. Densely distributed surface papillae on the head and along the lateral line are characteristic of many species of small-eyed fishes. The demonstrated agility of *B. hollisi* individuals (although not the holotype) indicates well-developed sensory perception of some kind.

Although *B. hollisi* has not been observed to feed, the possibility that the fish ingests bacterial masses was suggested by BALLARD and GRASSLE (1979), that it lives on microorganisms in the thermal fluid by GRASSLE (1985), and chemautotrophy has been suggested by HESSLER and SMITHEY (1984). The excised intestinal tract of our specimen is empty. The structure of the branchial arches, with few widely spaced gill rakers (Fig. 3), does not indicate filter feeding. The dentition is similar to that of other bythitids in general and three of the other known *Bythites* species in particular.

Virtually all fossil records of bythitids are from Cenozoic otoliths (NOLF, 1980). The only non-otolith fossil is *Propteridium*, a genus not far different from the nominal *Abythites*, from the Oligocene of Iran (COHEN and NIELSEN, 1978). Thus the family is apparently not of great antiquity. *B. hollisi* is not very different morphologically from other bythitids. Following the reasoning of NEWMAN (1985), the species (or its immediate forebears) is probably recently arrived at the vent habitat.

The relationships of the invertebrate fauna of the eastern Pacific vent systems have been reviewed by NEWMAN (1985 and personal communication). Although some 85 invertebrate species have been described, only three fish species, *Bythites hollisi*, *Thermarces cerberus*, and *T. andersoni* (ROSENBLATT and COHEN, 1986) are apparent vent endemics. Other fish species have been observed, but never in close association with the vents (COHEN and HAEDRICH, 1983; COHEN *et al.*, 1985). Even more striking is the disparity in endemism at higher taxonomic levels. Fully 60% of the genera and 45% of the invertebrate families are endemic.

Vents are an old feature of the ocean bottom (MALAHOFF, 1985), worm tube fossils have been reported from a Cretaceous hydrothermal vent deposit (HAYMON and KOSKI, 1985), and NEWMAN (1985) has argued persuasively for the antiquity of the extant invertebrate fauna of the vents. The fishes present a contrasting picture. *Thermarces* is a member of the advanced perciform suborder Blennioidei (ROSENBLATT, 1983) and *Bythites* is an ophidiiform. Bythitids and blennioids are known from the Eocene (60 my BP, NOLF, 1985). If the fishes were to resemble the invertebrates in relative phylogenetic position, one would have expected to find paleoniscoids (Paleozoic) or at least holosteans (Mesozoic). Instead we find two families of advanced teleosts and but three species.

Considering the near-ubiquity of fishes in marine environments, including the deep sea, and their dominant position as predators, their virtual absence from vent systems is at first glance puzzling. It may be argued that pre-teleost fishes never invaded the deep sea, but teleosts, members of a group that arose in the Triassic and radiated extensively in the Cretaceous, seemingly have had ample time to discover and exploit the rich food source represented by the vent ecosystem. It does not seem likely that elevated temperature was a factor. Although water coming from the very active vents known as smokers may be as hot as 350°C, it rapidly mixes with ambient seawater of 1–2°C (BAROSS and DEMING, 1955) and there is no reason to believe that the fishes need be living at more than a few degrees above normal deep-sea temperatures. However, in addition to its elevated temperature, vent water is characterized by a high concentration of sulfides, including hydrogen sulfide. Hydrogen sulfide is a potent poison that directly affects the nervous system as well as poisoning oxidative metabolism by binding to hemoglobin and inhibiting respiratory enzymes (NATIONAL RESEARCH COUNCIL, 1979). Some vent invertebrates have been shown to be resistant to elevated concentrations of H_2S, using a variety of methods to detoxify it (VETTER *et al.*, 1987). Invertebrates in general seem to be more resistant to H_2S (and anoxia) than vertebrates, perhaps because of less complex nervous systems and lower metabolic oxygen demands. It is interesting in this connection that another group of active predators, the Cephalopoda, is thus far unknown from the vent ecosystem. With no information available on the metabolism and biochemistry of vent fish, and so little known about effects of H_2S on marine fishes in general (NATIONAL RESEARCH COUNCIL, 1979), further speculation here does not seem profitable. Some estuarine and fresh water fishes do encounter low oxygen water and sulfide-rich sediments (ABEL, 1984), and investigation of their abilities to tolerate sulfide may, in conjunction with knowledge of the biochemistry of the fishes of the vents, provide an answer as to why there are so few kinds of vent fishes.

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REFERENCES

ABEL D. C. (1984) Terrestriality in the cyprinodontid fish *Rivulus marmoratus*: potential utility in H_2S and other bioassays. *Bulletin of Environmental Contamination and Toxicology*, **33**, 33–39.

ARAI R. (1969) *Bythites matsubarai*, a new brotulid fish from Japan. *Japanese Journal of Ichthyology*, **16**, 74–77.

BALLARD R. D. and J. F. GRASSLE (1979) Return to oases of the deep. *The National Geographic Magazine*, **156**, 689–703.

BAROSS J. A. and J. W. DEMING (1985) The role of bacteria in the ecology of black smoker environments. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 355–371.

BOEHLERT G. W. and M. M. YOKLAVICH (1983) Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. *Environmental Biology of Fishes*, **8**, 17–28.

BOEHLERT G. W., M. KUSAKARI and J. YAMADA (1987) Reproductive mode and energy costs of reproduction in the genus *Sebastes*. In: *Proceedings of the international rockfish symposium, Anchorage, Alaska, USA, October* 20–22, 1986, University of Alaska, Alaska Sea Grant Report 87-2, pp. 143–152.

COHEN D. M. and J. NIELSEN (1978) *Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the order*. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular no. 417, 72 pp.

COHEN D. M. and R. L. HAEDRICH (1983) The fish fauna of the Galapagos thermal vent region. *Deep-Sea Research*, **30**, 371–379.

COHEN D. M., R. H. ROSENBLATT and R. L. HAEDRICH (1985) Identity of thermal vent fishes in the eastern Pacific: an interim report. In: *The hydothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 229–230.

CORLISS J. B. and R. D. BALLARD (1977) Oases of life in the cold abyss. *The National Geographic Magazine*, **152**, 440–453.

CORLISS J. B., J. DYMOND, L. I. GORDON, J. M. EDMOND, R. P. VON HERZEN, R. D. BALLARD, K. GREEN, D. WILLIAMS, A. BAINBRIDGE, K. CRANE and T. H. VAN ANDEL (1979) Submarine thermal springs on the Galapagos Rift. *Science*, **203**, 1073–1083.

GEISTDOERFER P. (1988) Les peuplements ichthyologiques lies aux sites hydrothermaux et vivant a leur peripherie. *Oceanologica Acta*, **8**, 125–129.

GRASSLE J. F. (1985) Hydrothermal vent animals: distribution and biology. *Science*, **229**, 713–717.

HAYMON R. M. and R. A. KOSKI (1985) Evidence of an ancient hydrothermal vent community: fossil worm tubes in Cretaceous sulfide deposits of the Samail ophiolite, Oman. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 57–65.

HESSLER R. R. and W. M. SMITHEY (1984) The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents: In: *Hydrothermal processes at seafloor spreading centers*, P. A. RONA, K. BOSTROM, L. LAUBIER and K. SMITH, editors, NATO Conference Series IV, Vol. 12, Plenum Publishing Corporation, New York, pp. 735–770.

HESSLER R. R., W. M. SMITHEY, M. A. BOUDRIAS, C. H. KELLER, P. A. LUTZ and J. J. CHILDRESS (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galapagos Rift: eastern tropical Pacific). *Deep-Sea Research*, **35**, 1681–1709.

JANNASCH H. (1984) Microbial processes at deep-sea hydrothermal vents. In: *Hydrothermal processes at seafloor spreading centers*, P. A. RONA *et al.*, editors, NATO Conference Series IV, Vol. 12, Plenum, New York, pp. 677–709.

LUTZ R. A. and R. A. HESSLER (1983) Life without sunlight. *The Science Teacher*, **50**, 22–29.

MALAHOFF A. (1985) Hydrothermal vents and polymetallic sulfides of the Galapagos and Gorda/Juan de Fuca ridge systems and of submarine volcanoes. In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 19–41.

NATIONAL RESEARCH COUNCIL, SUBCOMMITTEE ON HYDROGEN SULFIDE, DIVISION OF MEDICAL SCIENCES (1979) *Hydrogen sulfide*. University Park Press, Baltimore, 183 pp.

NEWMAN W. A. (1985) The abyssal hydrothermal vent invertebrate fauna: a glimpse of antiquity? In: *The hydrothermal vents of the eastern Pacific: an overview*, M. L. JONES, editor, *Bulletin of the Biological Society of Washington*, **6**, 231–242.

NIELSEN J. G. and D. M. COHEN (1973) A review of the viviparous ophidioid fishes of the genera *Bythites* Reinhardt and *Abythites* new (Pisces, Ophidioidei). *Steenstrupia*, **3**, 71–88.

NOLF D. (1980) Etude monographique des otolites des ophidiiformes actuels et revision des especes fossiles (Pisces, Teleostei). *Mededelingen van de Werkgroep voor Tertiare en Kwartaire Geologie, Contributions to Tertiary and Quaternary Geology*, **17**, 7–195.

NOLF D. (1985) Otolithi piscium. In: *Handbook of Paleoichthyology*, H. P. SCHULTZE, editor, Vol. 10, Gustav Fischer Verlag, Stuttgart, 145 pp.

ROSENBLATT R. H. (1983) Blennioidei: introduction. In: *Ontogeny and systematics of fishes*, H. G. MOSER, editor, *Special Publication of the American Society of Ichthyologists and Herpetologists*, **1**, pp. 551–552.

ROSENBLATT R. H. and D. M. COHEN (1986) Fishes living in deep sea thermal vents in the tropical eastern Pacific, with descriptions of a new genus and two new species of eelpouts (Zoarcidae). *Transactions of the San Diego Society of Natural History*, **21**, 71–79.

SUAREZ S. S. (1975) The reproductive biology of *Ogilbia cayorum*, a viviparous brotulid fish. *Bulletin of Marine Science*, **25**, 143–173.

VETTER R. D., M. E. WELLS, A. L. KURTSMAN and G. N. SOMERO (1987) Sulfide detoxification by the hydrothermal vent crab *Bytheograea thermydron* and other decapod crustaceans. *Physiological Zoology*, **60**, 121–137.

WOURMS J. P. (1981) Viviparity: the maternal–fetal relationship. *American Zoologist*, **21**, 473–515.

Writing for Fishery Journals
American Fisheries Society 1990

We Don't Care, Professor Einstein, the Instructions to the Authors Specifically Said *Double*-Spaced

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Abstract.—You can ensure that your relations with a scientific editor will be adversarial by following three basic rules. (1) Submit a manuscript that is inappropriate for the journal. (2) Prepare the manuscript in a style that deviates—but not consistently—from accepted standards of form, syntax, and spelling, and submit barely legible photocopies. (3) When critical reviews are received, treat them as an affront to your professional image and respond accordingly. On the other hand, relatively little effort by you will contribute much toward establishing and maintaining cordial relations with the scientific editor. Being objective about your manuscript and choosing the appropriate outlet, preparing your submission copy carefully, and dealing constructively with the review–revision cycle will more than pay back the time invested. This should be obvious, but an amazing number of authors fail to pay such attention, and thereby prejudice the acceptance of their manuscripts.

For most scientific journals, the editor wields absolute power. For instance, answering to no one, the scientific editor has the power to reject your manuscript without review (''Dear Author, Although your manuscript dealing with an application of the unified field theory to age and growth in fishes seems interesting, I am afraid I have recently received several manuscripts on exactly the same subject . . . ''), the power to send your manuscript out to the most savage of reviewers (''Dear Dr. Legree, The author of the enclosed manuscript thinks it has merit . . . ''), and the power to interpret the comments of a reviewer in the worst possible light (''The reviewer, in raising the remote possibility that sunspots affect . . . , forces me to request that you repeat . . . '').

Given the potential of such egregious application of power and the somewhat capricious nature of the review process, it behooves you to cultivate and maintain cordial relations with the scientific editor. Short of stuffing $100 bills into the submission package, how do you do that? I, from the vast perspective of almost 2 years as a scientific editor for the *Fishery Bulletin,* and my colleague will advise you how to maintain a productive association with the scientific editor and thus facilitate publication of your manuscripts. Our purpose is to examine the submission–review–revise–acceptance process, concentrating on what we see as your responsibilities as author. We deliberately avoid discussing the responsibilities of the scientific editor. After all, when you deal with dictators, it makes good sense to avoid hectoring them about their shortcomings. If you violate certain basic, commonsense rules, you will find yourself dealing with an unenthusiastic, hostile, or ''imposed-on'' editor; none of these personas is conducive to rapid publication of your manuscript.

Choosing the Appropriate Outlet

To ensure that the scientific editor will be enthusiastic about receiving your manuscript, you must choose the appropriate outlet. Along with an exponential increase in the overall number of journals (there are now at least 40,000 scientific journals around the world: Garfield 1988), the number of serials related to fishery topics has also increased. From 3 to 17 new fishery titles have been added per year, worldwide, since World War II (Maclean 1988). With such a large selection, it should be easy to find a journal eager to publish your work. Presumably you know the length and content of your manuscript. (And, of course, it is competent science.) The difficulty is judging objectively its value as a contribution. Is it a data report from the results of a baseline survey or does it describe a fundamental conceptual advance? That is, what is its contribution level? Objectively judging your own work helps you to select the outlet; it is hardly productive to spend time arranging the data report of your baseline survey in the format and style for submission to *Science*. Most authors do not make such gross errors in judgment; nevertheless many authors seem unsure of the value of their manuscripts. We spend a substantial amount of time "previewing" manuscripts in response to authors doubtful of their contribution's appropriateness for our journal. For all but the most novice of authors, this step should be unnecessary and tends to prejudice the editor. When authors ask an editor if a manuscript is appropriate for a journal, they usually seem to be saying, "This may not be the most interesting manuscript in the world, but would you consider it anyway?" Or, "I know this is in miserable shape, but do you think it is worth more effort on my part?" The best course is to dispassionately judge the quality of your own manuscript and carefully choose a journal that you know, from past articles, publishes manuscripts of a similar contribution level. Never let a scientific editor see a product of yours that is not up to the quality of most of the manuscripts that he or she sees.

Choosing the appropriate journal requires that you know something about it. Familiarity with its content should help you decide. We assume you have read it. Is your manuscript similar in scope and contribution level to those published in recent issues? The policy statements in the instructions to authors also help. Have you read them? We suspect that a considerable number of authors neglect to do so. *Fishery Bulletin* gets a surprising number of manuscripts that include original drawings even though the instructions clearly state that they should not be sent until requested.

These preliminary investigations allow you to decide if the level of contribution of your manuscript is sufficient for the journal. The scientific editor will then support its publication, if not enthusiastically, at least neutrally. These investigations also help you put your contribution in perspective with other articles previously published in the same journal. It is important that this is made clear to the scientific editor. "My article is a logical extension of the questions raised by Blank et al. published in 19XX."

Now that you have decided that the prospective journal publishes papers similar to your contribution, is the journal itself adequate for your purposes? At the outset, we suspected that there might be three areas of interest to authors regarding potential outlets for their manuscripts: (1) circulation, (2) number of manuscripts submitted and rejected per year, and (3) journal impact or influence. The relationships (or the unexpected lack of them) that we discovered are

TABLE 1.—List of journals from which information was obtained on page charges, circulation size, number of manuscripts submitted per year, and proportion of manuscripts rejected. (The scientific editors or editorial assistants were contacted by telephone or letter.) Journals marked with an asterisk impose page charges.

American Zoologist
Aquaculture
*Biological Bulletin**
Bulletin of Marine Science
*California Fish and Game**
*Canadian Journal of Fisheries and Aquatic Sciences**
Canadian Journal of Zoology
*Copeia**
Environmental Biology of Fishes
Fishery Bulletin
*Journal of Crustacean Biology**
Journal of Fish Biology
*Journal of Mammalogy**
*Journal of Wildlife Management**
Journal of Experimental Marine Biology and Ecology
*Journal of Shellfish Research**
Limnology and Oceanography
Marine Biology
*Marine Mammal Science**
*North American Journal of Fisheries Management**
Physiological Zoology
*Progressive Fish-Culturist**
Science
*Systematic Zoology**
*Transactions of the American Fisheries Society**

intriguing, but the analyses have been left at a very superficial level. As a result, our interpretations are very speculative. Our goal was not so much to draw conclusions about the publishing process but rather to present information that an author might wish to investigate further and in greater depth for his or her own particular situation. We collected information by an informal telephone survey from the editors of various journals that American Fisheries Society scientists probably read and publish in (Table 1). The list is a casual selection of publications on our current journal library shelf. The editors or their editorial assistants were asked about page charges, individual and institutional circulation, number of manuscripts received per year, and the proportion of manuscripts rejected. We also consulted *Journal Citation Reports* (Institute for Scientific Information, Philadelphia, Pennsylvania) for data dealing with journal influence.

Page charges are like a regressive tax; their burden is greater on less well-funded programs. Consequently, investigators with poor funding may wish to avoid publishing in journals that impose page charges (Table 1). However, some editors of journals that impose page charges disclosed to us that an author can sometimes negotiate to have the charges reduced or eliminated.

Circulation may be important to an author wanting to do more than simply publish. Surveys show that scientists primarily read the journals to which they subscribe (G. Kean, Allen Press, Inc., personal communication), and neglect other journals in their institutional library. If this is true, authors seeking maximum exposure should publish in journals whose subscription fees are low and that consequently have developed large circulations to individual subscribers. In contrast are those journals that could be classified as "commercial," typified

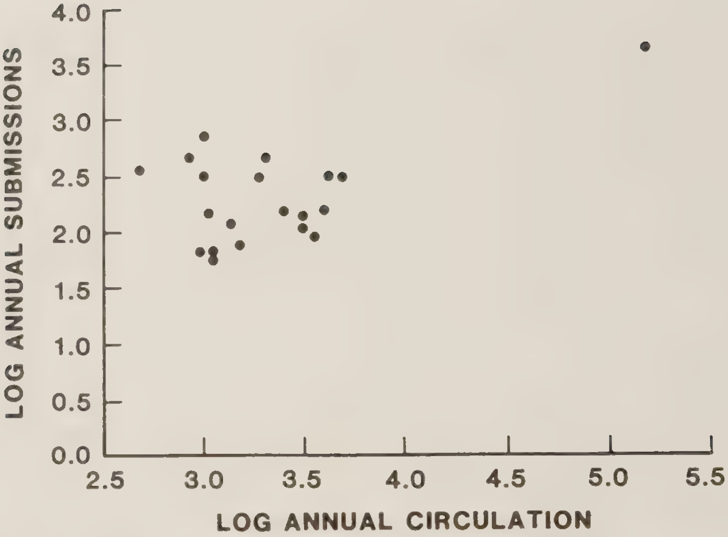

FIGURE 1.—Log_{10} annual circulation in number of issues versus $\log_{10}$ annual submissions in number of manuscripts for 20 scientific journals. *Science* is represented by the extreme point (total annual circulation = 150,000; total annual submissions = 4,000).

by *Aquaculture, Marine Biology,* and *Journal of Experimental Marine Biology and Ecology*. These are marketed to institutional subscribers, are very expensive (US$977, $1,683, and $1,300 in 1988 for the three journals just mentioned), and voluminous (24, 16, 30 issues per year). Circulation figures for these journals, and others like them, are confidential. Estimates of total circulation we obtained from a "knowledgeable source" were only 850 copies for *Aquaculture* and about 300 copies for *Environmental Biology of Fishes*. In contrast, *Science* has about 130,000 individual and 20,000 institutional subscribers. Specialty journals of societies, laboratories, and governments (at least in our survey) ranged from a high of 6,500 individual subscribers for *American Zoologist* to a low of under 50 for the *Canadian Journal of Zoology*. Most mature journals can assume an institutional circulation of 750 to 2,000 copies. Our journal, *Fishery Bulletin,* falls at the lower end; about 2,200 copies go to individuals and institutions combined.

We expected that scientists would want the maximum exposure possible for their articles and, therefore, would direct most of their manuscripts to journals with large circulations. However, for the journals in our survey (the ones for which we have information on submission and circulation), the number of annual submissions did not correlate with total circulation (Figure 1). Save for *Science,* with its large circulation and 4,000 unsolicited submissions each year, a large circulation does not seem to attract a large number of contributed papers. Seemingly, few scientists are concerned with circulation.

In contrast, rejection rate seems to be positively correlated with the number of annual submissions (Figure 2; $N = 20$, $P < 0.001$, $r^2 = 0.453$; Zar 1984). Again, *Science* provides an extreme value; of the 4,000 manuscripts received, editors can

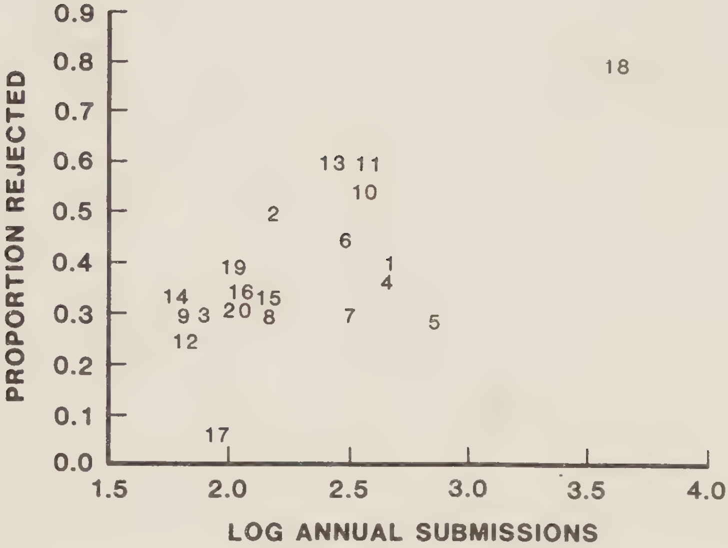

FIGURE 2.—Log_{10} annual submissions (number of manuscripts) to 20 scientific journals correlated with proportion of manuscripts rejected ($N = 20$, $P < 0.001$, $r^2 = 0.453$; Zar 1984). (1) *Aquaculture*, (2) *Biological Bulletin*, (3) *California Fish and Game*, (4) *Canadian Journal of Fisheries and Aquatic Sciences*, (5) *Canadian Journal of Zoology*, (6) *Copeia*, (7) *Environmental Biology of Fishes*, (8) *Fishery Bulletin*, (9) *Journal of Crustacean Biology*, (10) *Journal of Fish Biology*, (11) *Journal of Mammalogy*, (12) *Journal of Shellfish Research*, (13) *Limnology and Oceanography*, (14) *Marine Mammal Science*, (15) *North American Journal of Fisheries Management*, (16) *Physiological Zoology*, (17) *Progressive Fish-Culturist*, (18) *Science*, (19) *Systematic Zoology*, (20) *Transactions of the American Fisheries Society*.

reject 3,200 and still fill 52 issues per year. At the other extreme is *Progressive Fish-Culturist*, which rejects about 6 of its annual submissions of about 90 manuscripts. The *Canadian Journal of Zoology* deviates from the pattern somewhat in that it has 705 submissions per year and rejects only 29%.

Rejection rates for the sample of journals we used clustered around 30% (Figure 3). We do not know why. Perhaps scientists are capable of producing only two good manuscripts out of three, or, alternatively, every third scientist is incompetent. For *Fishery Bulletin*, we have no targets or guides on how many manuscripts we should reject, nor do we track or try to achieve any given figure. Nevertheless, we rejected 24% over the last 2 years, either immediately because they were inappropriate for the journal or after review. This percentage does not include "open" manuscripts, which require such extensive revision that they may never be resubmitted, or manuscripts that we requested be reduced to notes.

The influence of a journal can be estimated by various measures of the rate at which articles in that journal are cited. These analyses are provided by the *Journal Citation Reports*. One such measure is the "impact factor," a ratio of citations to citable items. It is the average frequency with which an article is cited during a particular year in other articles, both in the measured journal and in others. The measure for journal *X* for a given year, say 1984, is the number of 1984 citations

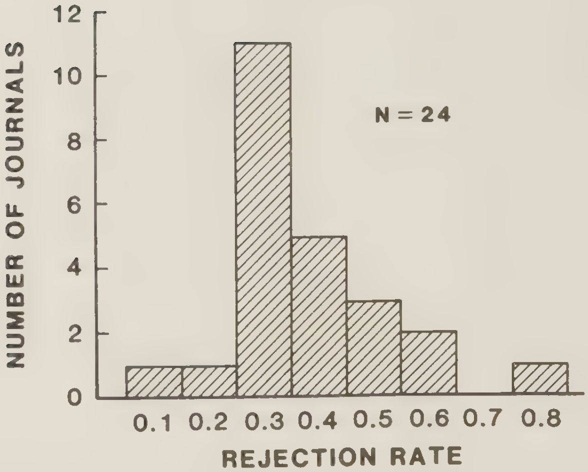

FIGURE 3.—Distribution of the proportion of manuscripts rejected by 24 of the 25 journals listed in Table 1.

everywhere to articles that had been published in journal *X* during the previous 2 years, 1983 and 1982, divided by the total number of citable articles published in journal *X* during those 2 years (Garfield 1972). The measure is biased by the size of the citing corpus and the choice of the 2-year window; this bias limits its utility for making comparisons between journals.

We examined the relation of impact factor to submission rate and, curiously, found that the two did not seem correlated (Figure 4). Once again *Science* is the exception, but journals such as *Limnology and Oceanography* and *Systematic Zoology*, whose subjectively perceived excellence is supported by high impact factors, are not distinguished by particularly high submission rates. Perhaps most scientists are unconcerned about the impact of their papers in terms of citability or, more likely, judge their contributions perceptively and avoid journals that would probably reject them.

Meeting Basic Standards

It is folly to increase the probability of a rejection by failing to meet the basic standards required of any scientific manuscript. By basic standards, we are not referring to scientific quality—that determination is somewhat more subjective. These are the standards, for the most part easily met, that dictate that a manuscript approximate the journal style, have easily readable text and prose, have legible and comprehensible figures and tables, and lack typographical errors. Nothing annoys a journal editor more than receiving a manuscript from an author who has obviously assumed that these details are unimportant.

The following admonitions may be reiterated by other authors in the present volume, but repetition will emphasize the point. Submitted manuscripts that meet the following criteria keep the scientific editor and the editorial staff reasonably happy and usually fare better than average in the reviewing process.

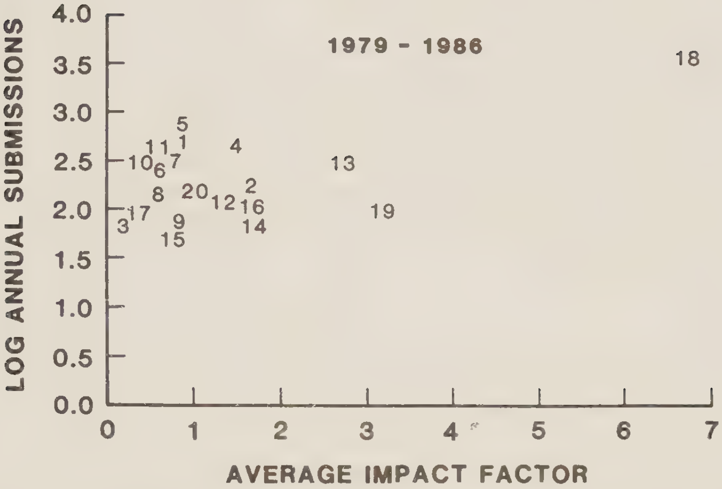

FIGURE 4.—Log_{10} annual submissions to 20 scientific journals versus average impact factor (number of citations per number of citable articles, from *Journal Citation Reports* 1979–1986). The following legend differs from that for Figure 2. (1) *Aquaculture*, (2) *Biological Bulletin*, (3) *California Fish and Game*, (4) *Canadian Journal of Fisheries and Aquatic Sciences*, (5) *Canadian Journal of Zoology*, (6) *Copeia*, (7) *Environmental Biology of Fishes*, (8) *Fishery Bulletin*, (9) *Journal of Crustacean Biology*, (10) *Journal of Mammalogy*, (11) *Journal of Wildlife Management*, (12) *Journal of Experimental Marine Biology and Ecology*, (13) *Limnology and Oceanography*, (14) *Marine Biology*, (15) *Marine Mammal Science*, (16) *Physiological Zoology*, (17) *Progressive Fish-Culturist*, (18) *Science*, (19) *Systematic Zoology*, (20) *Transactions of the American Fisheries Society*.

(1) The manuscript copy should approximate the style of the journal. It shows consideration for the copy editors and gives the scientific editor the impression that the manuscript was intended for his or her journal and was not rejected by some other journal. Approximating the specific style means that the copy editor will make fewer corrections on the copy. The more heavily a manuscript is marked, the more likely that errors will creep in during the typesetting process.

(2) The typography of the manuscript must be dark and legible and easily copied. Most manuscripts today are prepared on word processors; these should be output via a daisy wheel or laser printer. Do not submit a manuscript printed by a dot matrix printer; if you have no choice, use the emphasized or near-letter-quality mode with a new ribbon. Double-space all text, including the abstract, references, footnotes, and legends; they are edited too. Do not right-justify (i.e., do not create an even right margin); this adds extraneous spaces and makes the text harder to read. Do not hyphenate a word at the end of a line of typescript; ambiguous situations may occur. Indent each paragraph; if a new paragraph comes at a page break, it will be missed. Number each page; the frequency with which we get manuscripts without page numbers is surprising. Follow the guidelines of the American Mathematical Society for putting mathematics into print (Swanson 1979) and the CBE Style Manual (5th edition, 1983) for guidance.

(3) The manuscript must have readable prose (see Eschmeyer 1990 and Sinderman 1990, this volume). No more need be said.

(4) The manuscript must not contain unnecessary tables and figures (see Kennedy and Kennedy 1990, this volume). Ensure that the ones you include are comprehensible and well-designed. With the advent of inexpensive and easy-to-use computer graphics programs, more manuscripts include computer-generated figures and, perhaps as a result of the ease and low cost, include too many. Good biologists are not necessarily good graphic artists, and we believe that the quality of figures accompanying manuscripts has suffered as increasing numbers of biologists generate their own graphics with computers. Too many authors lose sight of the original goal of communicating information and get carried away with decorative graphical flourishes (fancy fonts, drop shadows, elaborate fill and grid patterns, shadow effects, exploding pie-wedges, etc.). Biologists producing their own figures should read "The Visual Display of Quantitative Information" by Tufte (1983), a remarkably readable and entertaining treatise on the historical evolution and proper design of statistical graphics.

(5) The manuscript must be proofread prior to submission. Take time with the preparation of the manuscript copy. The submission must be free of typographical errors and the style must be consistent throughout. Each manuscript copy must include all its tables and figures; although we at the *Fishery Bulletin* try to check each manuscript, incomplete copies occasionally are sent out to reviewers. We find it curious that a sizable minority of authors seems to feel that proofing copy is something that will be done by the journal editors, or that they will get to it after the review. They hope that reviewers will ignore these "trivial" matters and concentrate on the science. But sloppy manuscript preparation annoys the editors because it increases their work. It is also a red flag to reviewers; if the author is negligent with these details, reviewers often assume (and often correctly) that the carelessness carries over to the science. Reviewers are remarkably (and justifiably) harsh on authors of slipshod manuscripts.

In summary, the time spent carefully polishing a manuscript is trivial compared to the time spent collecting the data, analyzing them, and writing and editing the drafts. We think that a final polishing pays large dividends when a paper is reviewed and when the editorial decision about its publication is made.

Dealing with Reviewers' Comments

We assume that all scientists want the results of their research published, but we are not so naive as to think that their only motivation is a desire to communicate knowledge. Due to a variety of pressures, the act of publishing is itself a goal. We believe that it is important to recognize this as a modern reality; however, this need sometimes threatens the good judgment of authors about what constitutes merit in a contribution and makes them reluctant to accept negative criticism. ("I don't care if it's bad, I *have* to publish it.")

Ideally, authors should be as critical of their own manuscripts as anonymous reviewers are; however, this degree of self-criticism is unlikely. This unlikelihood and the pressures to publish makes an expert review system necessary. Thus, even if you are ill-served by a review, you still should recognize that the system is important, and treat the process with some degree of respect. It is not perfect, but better alternatives have not emerged.

Because most journals are multidisciplinary, their scientific editors depend heavily on the reviewers' recommendations. For the *Fishery Bulletin*, we attempt to get reviews from workers who are currently active in the subject field and who (we hope) are vitally interested in the subject matter. We trust that the solicited reviews are conscientious, informed, and thorough, because the verdict of the reviewers usually determines the final disposition of the manuscript. By and large, the system works. Our experience has been that most reviews are competent, and most authors find value in the comments of the reviewers.

Still, it is rarely pleasant to receive criticism, and criticism is sometimes applied with a heavy hand. From our observations, reviewers seem to develop a certain degree of hostility or righteous indignation toward manuscripts. This is understandable because reviewing manuscripts is an imposition with little reward. Most reviewers do not take on the persona of the wise teacher dispensing only constructive criticism. The perfectly normal, hostile emotions that the reviewer experiences fuel the search for error. The effectiveness of this hostility is borne out by the difference in quality between the reviews you the author solicit from your friends and colleagues (reviews that are often worthless or, if of value, too easy to ignore) and the ones supplied by the shadowy figures hiding behind the scientific editor. It is the anonymous reviews that reveal the weakness of the approach or the error in the methodology.

The fiendish joy that the reviewer experiences in finding flaws sometimes is apparent in the written comments that the author sees. The editor has considerable responsibility to maintain civility during the proceedings, but he or she is not always successful at winnowing out all potentially insulting comments. Some authors are insulted by the tone and hyperbole of such comments. This is somewhat puzzling; most authors have been reviewers, and many, if not all, have skewered an author or two themselves. In all situations, we suggest that the content of reviews, rather than the tone, be considered. Understanding what motivates the reviewer helps you ignore the hyperbole.

Besides resorting to snide hyperbole, reviewers sometimes are wrong and suggest poor revisions, and scientific editors sometimes pass these bad suggestions back to you. This gives you ample opportunity, in your resubmission covering letter, to indignantly pay back a career's worth of slights by all of the anonymous reviewers who have flayed your previous papers. Don't do it. Sometimes the scientific editor passes your sarcastic comments back to the reviewer—to whom you are not anonymous.

Handle the situation like this. Carefully evaluate all of comments of the reviewers and scientific editor. Handle those with merit, and look again at those without. In some instances, even wrong assertions or suggestions by the reviewers or scientific editor reveal a weakness in your argument or analysis. Reviewers are proxies for future readers. When they are confused, it is usually because of the author's bad writing. If, in a final dispassionate analysis, you conclude that the reviewer and scientific editor are simply wrong, be diplomatic even though this courtesy may seem one-sided. (After all, although the reviewer gets no real credit for a difficult job, you may end up with a published paper.) With your revised manuscript, you should write an accompanying letter indicating that you have carefully considered the reviewer's concerns and briefly noting how you handled each. For things that you are not willing to change (the objection is wrong, inappropriate, or stems from legitimate scientific differences), state why but keep the dialogue brief. We eventually published a manuscript dealing with fishery economics by an author whose rebuttal to a reviewer's comments was three times as long as the manuscript itself.

The scientific editor is occasionally caught in the middle of an apparently irreconcilable conflict between an author and an anonymous reviewer. In that situation, new reviewers are in order—some of whom might be suggested by you, the author. Additional reviews usually resolve the conflict; however, they can lead to contradictory advice, especially if the manuscript has gone through several review cycles. We have sometimes been embarrassed when the advice of new reviewers contradicts the advice that we have been dispensing on the basis of the original reviewers' concerns.

Sometimes the process goes totally awry. Our last warning to you is to avoid berating the scientific editor or journal about how poorly you were served by the process. In 2 years, we have had two irate authors who let us know exactly how they felt. Both swore they would never publish in the *Fishery Bulletin* again. One was mad because we rejected his manuscript. The other was mad because, although we accepted the manuscript, our reviewers were too slow at their jobs (actually, the delays were largely on the author's end). Revenge is sweet, but short-lived. Getting published is too important and too difficult for you to jeopardize future chances by eliminating outlets and alienating colleagues.

As we said in the beginning of this section, the peer-review process is not a perfect system—just a necessary one.

References

CBE Style Manual Committee. 1983. CBE style manual, 5th edition. Council of Biological Editors, Inc., Bethesda, Maryland.

Eschmeyer, P. H. 1990. Usage and style in fishery manuscripts. Pages 1–25 *in* J. Hunter, editor. Writing for fishery journals. American Fisheries Society, Bethesda, Maryland.

Garfield, E. 1972. Citation analysis as a tool in journal evaluation. Science (Washington, D.C.) 178:471–479.

Garfield, E. 1988. Too many journals? Nonsense! The Scientist 2(5):11. (Institute for Scientific Information, Philadelphia, Pennsylvania.)

Kennedy, V. S., and D. C. Kennedy. 1990. Graphic and tabular display of fishery data. Pages 33–64 *in* J. Hunter, editor. Writing for fishery journals. American Fisheries Society, Bethesda, Maryland.

Maclean, J. L. 1988. The growth of fisheries literature. Naga, the ICLARM Quarterly 11(1):3–4. (International Center for Living Aquatic Resources Management, Manila.)

Sindermann, C. J. 1990. Scientific writing as English prose. Pages 75–78 *in* J. Hunter, editor. Writing for fishery journals. American Fisheries Society, Bethesda, Maryland.

Swanson, E. 1979. Mathematics into type, revised edition. American Mathematical Society, Providence, Rhode Island.

Tufte, E. R. 1983. The visual display of quantitative information. Graphics Press, Cheshire, Connecticut.

Zar, J. H. 1984. Biostatistical analysis, 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey.

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PARTURITION IN THE HAWAIIAN MONK SEAL (*MONACHUS SCHAUINSLANDI*)

Parturition in the Hawaiian monk seal (*Monachus schauinslandi*) has never been described in detail and has rarely been witnessed. Only four complete births (Johnson and Johnson 1978, C. J. Deutsch, personal communication, A. K. H. Kam, personal communication, J. Ruehle and A. M. Johnson, unpublished data) and two partially observed births (Alcorn 1984, Johanos and Kam 1986) have been reported. Herein we recount two births observed in 1985 in the Northwestern Hawaiian Islands, and we include the first sonograms of postpartum vocalizations between a mother-pup pair. Parturition behaviors of Hawaiian monk seals are summarized from all reported births to date.

The birth of a female pup was witnessed by two observers, 10–15 m away from the parturient female, at East Island in the French Frigate Shoals (23°47′N, 166°13′W) on 24 April 1985. When first observed at 1429, the parturient female was at the water's edge, 3–4 m from two basking Hawaiian green turtles (*Chelonia mydas*). She appeared to be experiencing occasional, mild labor contractions that spread posteriorly from the midbody region.

Observations resumed at 1502. From then until the birth, 22 contractions were observed, with intervals of 15–328 sec. During labor, the female frequently changed her position by alternately lying on her ventrum and side. When lying on her ventrum, she slightly arched her lower back during contractions, elevating her pelvic area and hind flippers 8–10 cm from the ground while slightly spreading her hind flippers. When lying on her side, she raised the upper hind flipper 6–8 cm from the lower hind flipper. As the contractions intensified during the later stages of labor, the seal also stretched her body forward with the contractions. She occasionally moved along the beach for short distances and emitted low-pitched "moaning" vocalizations or low guttural growls, which were similar to vocalizations often emitted by mothers to attract their pups. The seal vocalized at a Laysan albatross (*Diomedea immutabilis*) flying overhead. She also thrust her head towards one of the basking turtles and vocalized at both turtles several times, after which one entered the water.

Dilation of the vaginal aperture was first observed 15 min before parturition. The seal lay on her side, with the amniotic sac protruding approximately 5 cm. Six minutes later, amniotic fluid was expelled, and 10–12 cm of the amniotic sac was visible. The sac was withdrawn briefly 6 min before parturition; 25% and then 30–50% of the sac protruded from the vaginal aperture 1 and 2 min later, respectively. The seal repositioned to lie on her ventrum with her hind flippers draped over a small berm and angled slightly downward at the water's edge. The pup, enclosed in the amniotic sac, was expelled at 1527.

Presentation was caudal. The umbilicus separated and amniotic sac broke away from the pup as the pup was expelled into the breaking waves. The mother immediately turned, aggressively bit her pup, and vocalized. We saw no evidence of injury to the pup during this interaction. When a wave washed the pup against its mother, she nosed her pup for the first time. The pup then emitted its first vocalization, an abrupt bleat.

After a brief interruption from 1530 to 1533, observations continued until 1818. During this period, waves repeatedly separated the mother-pup pair and rolled the pup back and forth at the shoreline. The mother rolled onto her side and the placenta partially emerged 22 min postpartum; however, it remained attached for an additional 14 min. She presented her ventrum toward the pup 29 min postpartum, presumably to solicit nursing. She presented an additional seven times; however, no suckling occurred. Vocalization by the mother was associated with presentation five out of eight times, and nosing by either the mother or pup was associated with presentation four out of eight times. The mother lunged toward her pup 14 more times, 5 of which involved aggressive biting. She also hit the pup with her foreflipper on five different occasions while presenting to the pup and purposely or inadvertently "restrained" the pup nine times by resting her foreflipper, head, or body over the pup. The pup struggled unsuccessfully to free itself from under its mother and bit her on the muzzle during one period of restraint. The mother nosed her pup 93 times, and the pup nosed its mother 39 times. The total number of nose contacts by either the mother or pup for each 15-min period after birth ranged from 5 to 24 and showed no relationship with time; however, the pup was repeatedly washed away from its mother by breaking waves.

The mother-pup pair was approached by swimming seals seven times during the observation period. The mother usually vocalized and nosed her pup when the seals approached; however, once she lunged at the pup and vocalized. The approaching seal fled in each case.

Sound spectrograms of the mother and pup vocalizations are presented in Figure 1. Tape recordings were made with a Nagra IS[1] tape recorder and a Sennheiser MKH816 "shotgun" microphone with Scotch audio tape 208, at a speed of 19 cm/sec. Signals were digitized at a rate of 10,000 Hz, and a Hamming window was used, pre-emphasis (factor, 0.98), low smoothing (*i.e.*, incorporating four bins on either side of the current bin) and 1,024 points for each analysis. The duration of each sample was 102.4 milliseconds (1,024/10,000 Hz). The mother's calls were loud low-frequency "bawls," each about 1 sec long. Pup calls were weaker, higher pitched, and spanned a broader frequency range.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

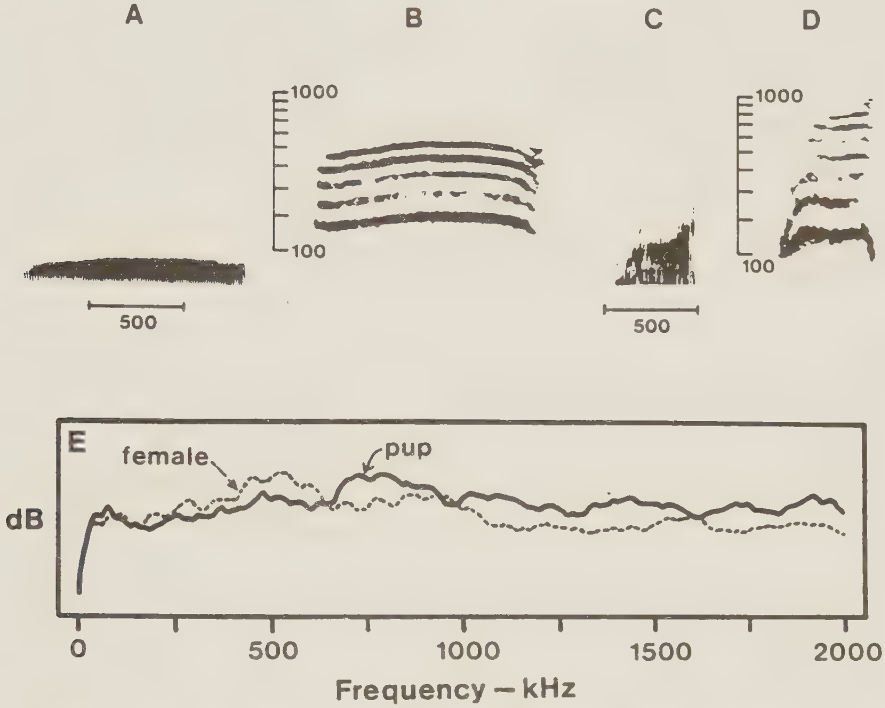

Figure 1. Analysis of vocalizations of a female monk seal and her newborn pup. (*A*) Sound spectrogram of a female call analyzed over the range 40–4,000 Hz, with analyzing filter bandwidth of 150 Hz and linear frequency scale. Time marker, 500 milliseconds. (*B*) Sound spectrogram of same call, analyzed over the same range, with analyzing filter bandwidth of 22.5 Hz and logarithmic frequency scale (in Hz). (*C*) Sound spectrogram of pup call, analyzed as in *A*. (*D*) Sound spectrogram of pup call, analyzed as in *B*. (*E*) Power spectra of 102 millisecond segments from central parts of preceding calls. The two calls were recorded under different conditions; therefore, their sound levels are not comparable.

Both mother and pup continued to vocalize throughout the observation period. The pup vocalized several times when "restrained" by its mother, and intermittently as it struggled against the breaking waves. Pup calls often followed the mother's calls and vice versa. Nosings by either the mother or pup also occurred frequently before or after the calls.

The birth of a male pup was witnessed by four observers located 25 m away from the parturient female, at Laysan Island (25°42′N, 171°44′W) on 28 April 1985. Two days earlier, the female had hauled out and then remained in the vicinity of her parturition site. She was checked intermittently for signs of labor. The interval between the 1984 and 1985 parturition dates for this female was 376 days. At 0800 labor was not evident. When the female was checked at 0930 contractions were observed. The seal lay on her right side, approximately 8 m from the water. An adult male seal was near the water approximately 10 m away.

Table 1. Summary of observed *Monachus schauinslandi* births (FFS = French Frigate Shoals).

Observations	Ruehle and Johnson (unpublished data)	Johnson and Johnson (1978)	Kam (personal communication)	Deutsch (personal communication)	Alcorn (1984)	Johanos and Kam (1986)	FFS 1985 (this study)	Laysan Island 1985 (this study)
Date	2 Mar. 1977	1977	5 May 1982	12 May 1982	1982	13 May 1983	24 Apr. 1985	28 Apr. 1985
Island	Kure	Laysan	Laysan	East, FFS	Laysan	Lisianski	East, FFS	Laysan
Observation time	1012–1245	—	2325–0021	0742–0805	—	—	1502–1818	1001–1050
Birth time	1013	1830	2325	0747	—	1440–1503	1527	1007
Entire birth observed?	Yes	Yes	Yes	Yes	No	No	Yes	Yes
Position	Lateral	—	Lateral	Lateral	—	—	Ventral	Lateral
Vaginal dilation[a]	—	—	—	—	—	—	15	3
Pup presentation	Cephalic	Caudal	Cephalic	Cephalic	—	—	Caudal	Cephalic
Labor duration[b]	—	30	55[c]	—	—	—	58[d]	37[d]
Delivery duration[e]	—	—	—	3–5	—	—	15	1
Amniotic sac broke	At birth	—	Before birth	At birth	—	—	9[a]	At birth
Placenta expelled[f]	At birth	—	45	1–6	43	0–23	22	8
Umbilicus broke[f]	5	—	2	18–49	—	2–25	At birth	At birth
Female vocalize	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Pup vocalize	—	Yes	Yes	Yes, once	—	Yes	Yes	Yes
Nursing presentation[f]	19	—	—	—	—	—	29	21
Nurse[f]	47	90[d]	56[d]	18–51	210[d]	180[d]	171[d]	43[d]

[a] Minutes before birth.

[b] Labor duration (in minutes) is the interval between the onset of observed labor contractions and birth.

[c] Maximum time.

[d] Minimum time.

[e] Delivery duration (in minutes) is the interval between first appearance of the amniotic sac and final expulsion of the pup.

[f] Minutes after birth.

Observations resumed at 1001. From then until the birth, the mean interval between contractions was estimated at 30 sec. During contractions, the seal flexed and elevated her pelvic area 10–20 cm from the ground, spreading her hind flippers. No other movements were observed, and no vocalizations were heard. Dilation of the vaginal aperture was first observed 3 min before parturition. The seal then became very restless; she looked around several times and emitted low-pitched guttural growls. Birth occurred at 1007: the pup's head emerged, covered by the amniotic sac. A few seconds later, the female lifted and twisted her hindquarters approximately 30 cm off the ground, expelling the pup. Labor lasted a minimum of 37 min. The interval between first emergence of the amniotic sac and birth was approximately 1 min.

Presentation was cephalic. As the pup was expelled, the amniotic sac tore immediately, exposing the pup's head. The mother vocalized repeatedly, using low-pitched guttural growls, and nosed the pup's muzzle. Two minutes postpartum, the pup crawled completely out of the amniotic sac and approached the mother's head. The umbilical cord was no longer attached to the pup.

The mother and pup nosed each other frequently. The female vocalized repeatedly at the pup and also at the adult male seal nearby. She had periodic contractions during this time, and the placenta partially emerged 8 min postpartum; however, it remained attached throughout the observation period. The pup emitted its first vocalization 12 min postpartum, after the mother and pup nosed each other. The mother rolled onto her side 21 min postpartum and presented her ventrum to the pup for the first time. She presented three more times, but the pup did not suckle, although it nosed her ventral area. Once, immediately preceding her presentation, the mother used a single motion of her foreflipper to flip the pup from her head region to her nipple area. At no time did the mother lunge at or bite her pup. Observations ended at 1050.

Although these two births were observed during daylight hours, many monk seal births apparently occur at night. Approximate times of parturition were determined in 29 births at French Frigate Shoals from 1983 to 1985 by searching for newborn pups during morning and evening island patrols, periodic censuses, and miscellaneous observations. Twenty-one of these births (72%) most likely occurred at night or early in the morning (J. Eliason, J. Henderson, and M. Webber, unpublished data). Five out of nine births probably occurred at night on Lisianski Island in 1983 (Johanos and Kam 1986).

A summary of all completely and partially observed births reported for the Hawaiian monk seal is presented in Table 1. Based on a limited number of observations, a typical monk seal birth can be described as follows: Labor begins sometime during the night or early morning, the pup is expelled head first while the female lies on her side, and the amniotic sac and umbilicus break at birth or shortly thereafter. The mother and pup exchange frequent vocalizations, and the pup does not nurse immediately after birth.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALCORN, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-42. 32 pp.

JOHANOS, T. C., AND A. K. H. KAM. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-58. 37 pp.

JOHNSON, B. W., AND P. A. JOHNSON. 1978. The Hawaiian monk seal on Laysan Island: 1977. U.S. Department of Commerce, National Technical Information Service, Springfield, Va., PB-285-428. 38 pp.

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Maturation and Reproduction in Two Hawaiian Eteline Snappers, Uku, *Aprion virescens*, and Onaga, *Etelis coruscans*

Alan R. Everson, Happy A. Williams, and Bernard M. Ito

ABSTRACT: Size at sexual maturity, spawning season, and pattern of egg release were determined for two of Hawaii's commercially important snapper species: uku, *Aprion virescens*, and onaga, *Etelis coruscans*. Sexual maturity of females was assessed by macroscopic and microscopic (oocyte measurement and histology) techniques and gonosomatic indexes. Interspecific differences were noted in many aspects of the reproductive biology. Both species had protracted spawning seasons: uku spawned in May-October while onaga spawned in June–November. Female size at sexual maturity was 425–475 mm fork length (FL) for uku and 675–725 mm FL for onaga. Both species were determined to be multiple spawners, although the number of batches spawned per season could not be established.

Uku, *Aprion virescens*, and onaga, *Etelis coruscans* (Lutjanidae), are species of considerable importance in terms of total landings and value to bottom fish fisheries in southern Japan (Masuda et al. 1975), Guam, the Northern Marianas (Amesbury and Myers 1982), Vanuatu (Brouard and Grandperrin 1985), American Samoa (Western Pacific Regional Fishery Management Council (Council) 1986), and Hawaii (Ralston and Kawamoto[1]). In addition, many other Pacific island nations have subsistence and commercial fisheries for these species. In Hawaii, uku and onaga ranked second and third, after *Pristipomoides filamentosus*, in total catch and value among bottom fish species in 1984 (Pooley 1987).

Both species are widely distributed throughout the tropical Indo-Pacific. Uku range from East Africa to Hawaii and from southern Japan to Australia (Allen 1985), and onaga extend to the Atlantic coasts of South America and Africa (Druzhinin 1970). Uku are caught at the surface by trolling gear and at ≤ 300 m depths by deep-sea handline gear (Druzhinin 1970), whereas onaga are restricted to deeper waters between 220 and 320 m. In Hawaii, the greatest portion of the uku and onaga catches comes from the Penguin Bank region, which is southwest of Molokai in the main Hawaiian Islands (Ralston[2]).

Relatively few reproductive studies have been completed for the commercially important bottom fishes of the western Pacific, even though such information represents a critical component of the biological basis of management for the bottom fish and seamount groundfish fisheries in this region (Council 1986). Some information is available on Hawaiian stocks of *P. filamentosus* (Ralston 1981; Kikkawa 1984), *Etelis carbunculus* (Everson 1984), and *Seriola dumerili* (Kikkawa and Everson 1984), but none is available for uku and onaga. Thus, a study was undertaken to determine the size at sexual maturity, spawning season, and pattern of egg release of uku and onaga. Size at sexual maturity is a particularly important parameter used to assess and evaluate the impact of fishing mortality on spawning stock biomass and to determine levels of optimum fishery yield (Polovina 1987). During this study, we also attempted, within the constraints imposed by our sampling program, to develop an efficient method for determining gonad maturity. A third goal was to discern interspecific differences between the reproductive biology of the two species and to interpret those differences.

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[1] Ralston, S., and K. E. Kawamoto. 1987. An assessment and description of the status of bottom fish stocks in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-7, 55 p.

[2] Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822–2396.

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MATERIALS AND METHODS

Uku and onaga caught in 1984–86 and 1985–87, respectively, by commercial fishermen using deep-sea hook-and-line gear were weighed and measured for fork length (FL), and their capture locations were noted. Most were caught in the main Hawaiian Islands and were sold through the Honolulu wholesale fish auction. Following sale of the fish, viscera were extracted by the purchasing agent and refrigerated with an identifying tag. Gonad samples were collected later and preserved at the laboratory either in modified Gilson's fluid (Bagenal and Braum 1968) or Bouin's fluid.

Sexual maturity of females was evaluated by several methods. First, ovaries were staged macroscopically and given a preliminary maturity stage designation (Hilge 1977) (Table 1). To refine and confirm these macroscopic designations, at least one of the following three additional microscopic techniques was used: volumetric or cork borer subsampling, which is based upon the size and appearance of individual oocytes, or standard histological examination. Hilge's (1977) table was also used to assign a final stage designation to these ovaries. To avoid confusion, prespawning adults prior to vitellogenesis were classified as stage I immature, and prereproductive individuals as stage I juvenile.

To determine oocyte size-frequency distributions by volumetric subsampling, uku ovaries preserved in modified Gilson's fluid were examined. After adequate time for dissolution, connective tissues were removed, and the remaining "free" ova were placed in a flask, which was then filled with 200 mL of water. A homogeneous distribution of ova was obtained by using a magnetic stirrer (Van Dalsen 1977). A 3 mL sample was then pipetted onto a gridded petri dish and examined under a binocular dissecting scope at 50×. With an ocular micrometer, 100–200 oocytes were measured along their longest dimension. This method precluded the need to measure oocytes from various sites within the ovary to determine spatial homogeneity of development. Maturity stages were assigned based upon the largest oocyte mode and the degree of oocyte transparency (Table 1).

Subsamples of ovaries of both species preserved in Bouin's fluid were taken from the anterior portion with a cork borer and examined under a binocular dissecting microscope at 50×. The average diameter of the largest oocyte mode was determined, and the percentage of each maturity stage present was noted. Oocyte diameter frequency plots were constructed for uku ovaries in various stages of development and compared with similar plots constructed by using oocyte diameter data obtained by the volumetric method.

For histological examination, some ovaries of both species representing various visually identifiable maturity stages were transferred from Bouin's fluid to 70% ethanol. Portions of ovaries from 28 uku and 22 onaga caught at various times of the year were embedded in paraffin, sectioned at 5 μm, stained with hematoxylin, and counterstained with eosin. Each was as-

TABLE 1.—Ovary developmental stage designations used for study of the reproductive cycle of uku and onaga. Designations are adapted from Hilge (1977).

Class	Stage	Oocyte developmental status	Gonad external appearance	Stage classification criterion
I	Immature	Oogenesis from oogonium to primary oocyte with cytoplasmic vacuoles beginning to appear	Genit ridge to definite gonad; individual eggs not discernible	Oogonia transparent; primary ooctes translucent
II	Developing	Vitellogenesis	Elongation of the ovary	Opaque yolked oocytes
III	Ripe	Hydration	Swollen; ovary wall thin	Transparent, ripe ova
IV	Spent	Atresia, general cell breakdown	Slack; shrinking ovary; ovary wall thick	Residual ova

signed a maturity stage based on the criteria in Table 1. Oocytes were histologically identified using information provided in Crossland (1977). Sectioned ovaries also were examined for the presence of postovulatory follicles and oocyte atresia, features used to establish criteria for the estimation of spawning frequency and to separate juveniles from prespawning adults for determination of size at sexual maturity (Hunter and Macewicz 1985).

The results of these four visual methods were compared with gonosomatic index (GSI) values [(gonad weight/body weight) × 100]. Gonosomatic indexes were calculated for both species to provide a rapid but preliminary indication of developmental stage, although an insufficient number of uku testes were obtained. Excluded from this analysis were individuals that had not yet reached size at sexual maturity. Spearman's coefficient of rank correlation (Snedecor and Cochran 1978) was used to ascertain whether a positive relationship existed between GSI and maturity stage during the spawning periods for females of each species.

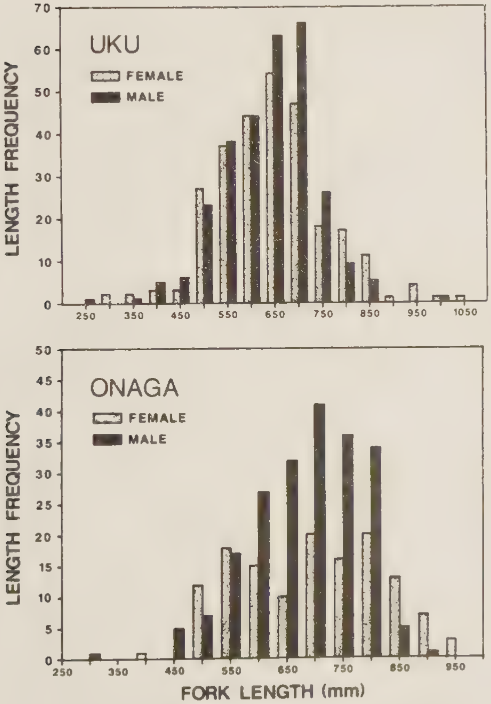


FIGURE 1.—Length-frequency distribution of male and female uku and onaga.

Size at sexual maturity (L_{50}) was defined as the smallest length category in which at least 50% of the individuals were mature (i.e., stage II or beyond, GSI > 1.5) during the spawning season. The logistic equation was fitted to the percentage of mature individuals in each size class (P_x) and FL (Gunderson et al. 1980; Ni and Sandeman 1984); that is

$$P_x = \frac{100}{1 + \exp(a\mathrm{FL} + b)},$$

where a and b are fitted parameters and $L_{50} = -b/a$. We also calculated the percentage of maximum length (MAXLEN) at which sexual maturity occurred. This ratio has been used to compare proportionate size at maturity for species by habitat type, zoographic province, or depth range (Grimes 1987).

Sex ratios were compiled and examined for significant deviation from unity and to determine whether sex ratio and size (in 50 mm FL intervals) were independent using chi-square statistics. Two-way contingency table analysis was performed to determine whether the sex ratio differed during the year when pooled into bimonthly periods.

RESULTS

Spawning Season

Spawning season was determined from a wide size range of uku and onaga (Fig. 1). The Spearman rank correlation coefficients (r_s) calculated by comparing GSI with stages I–III were $r_s = 0.6205$ for uku ($P < 0.0001$), and $r_s = 0.8685$ for onaga ($P < 0.0001$), indicating a positive relationship between GSI and stage of development for both species, although the correlation was considerably lower for uku. In addition, the range in GSI values representing stages II and III ovaries was greater for uku than for onaga (Fig. 2). Thus, rather than using GSI as the single method for estimating spawning seasonality by month or fish length, visual staging methods also were used.

Both species reached maturity in the spring and summer and spawned continuously until fall or early winter. Neither species reached stage II of development (vitellogenesis) at any other time of the year. Uku spawning began in May and peaked 1 month later in June, as evidenced by the sharp rise in GSI values and the presence of mature and ripe fish during this time (Figs. 3, 4).

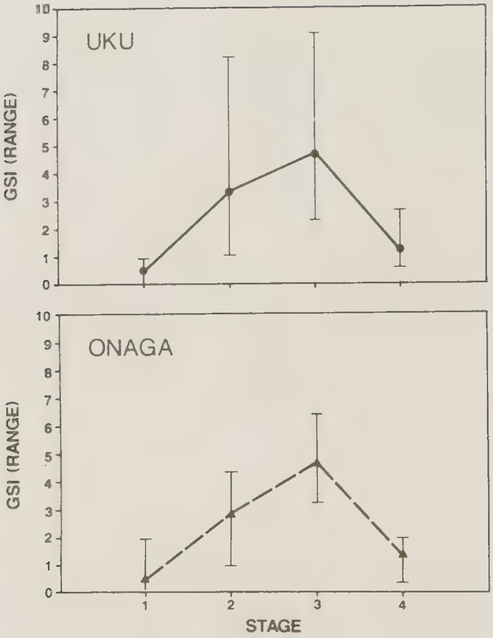


FIGURE 2.—Range in (A) uku and (B) onaga gonosomatic index (GSI) for each developmental stage designation in Table 1.

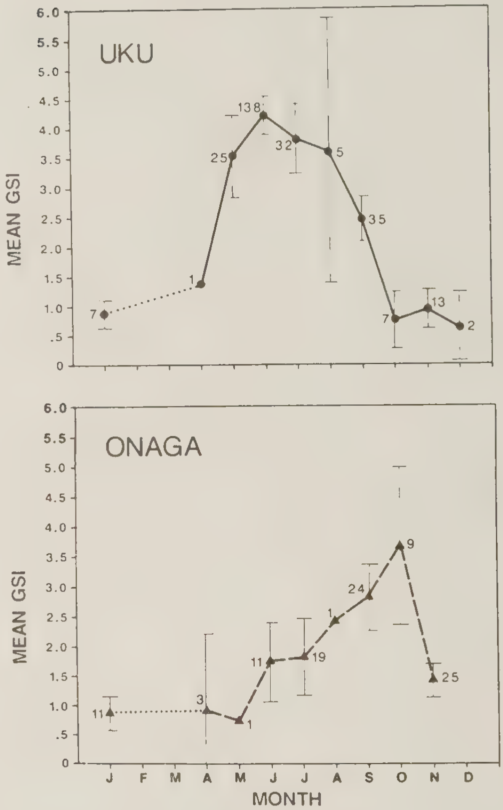


FIGURE 3.—Monthly mean gonosomatic index (GSI) for female uku and onaga. Bars indicate 95% confidence limits. Juvenile (<500 mm FL) uku and juvenile (<600 mm FL) onaga were excluded from analysis. Sample size is indicated next to each data point.

From July to October, the mean GSI values gradually decreased as spawning activity tapered off. By November, all fish examined were either partially or completely spawned (stage IV). Stage IV fish were not found during the spawning season.

In contrast, female onaga began maturing in June. Fully ripe onaga were not found until July, and spawning activity did not peak until October (Figs. 3, 4). The GSI values dropped sharply in November as the incidence of completely spawned and partially spawned individuals abruptly increased. As with uku, completely spawned individuals were not found until the close of the spawning season. Mean monthly GSI values for male onaga reflected a similar pattern.

Size at Sexual Maturity

Uku matured at a substantially smaller size than onaga. Fifty percent of the female uku attained sexual maturity at 425–475 mm FL, as evidenced by elevated GSI's (Fig. 5) and by the percentage of fish judged mature by visual staging (Table 2). By the time the fish reached the

TABLE 2.—Stage of maturity, compared by 50 mm fork length (FL) size classes, for uku and onaga sampled during their respective spawning seasons.

Uku			Onaga		
FL (mm)	*N*	Percentage mature	FL (mm)	*N*	Percentage mature
275–324	2	0	475–524	11	9
325–374	1	0	525–574	15	7
375–424	2	0	575–624	12	33
425–474	3	66	625–674	4	25
475–524	12	100	675–724	13	77
525–574	21	100	725–774	13	92
575–624	18	95	775–824	16	100
625–674	20	95	825–874	6	100
675–724	15	94	875–925	5	100
725–774	4	100			
775–824	5	100			

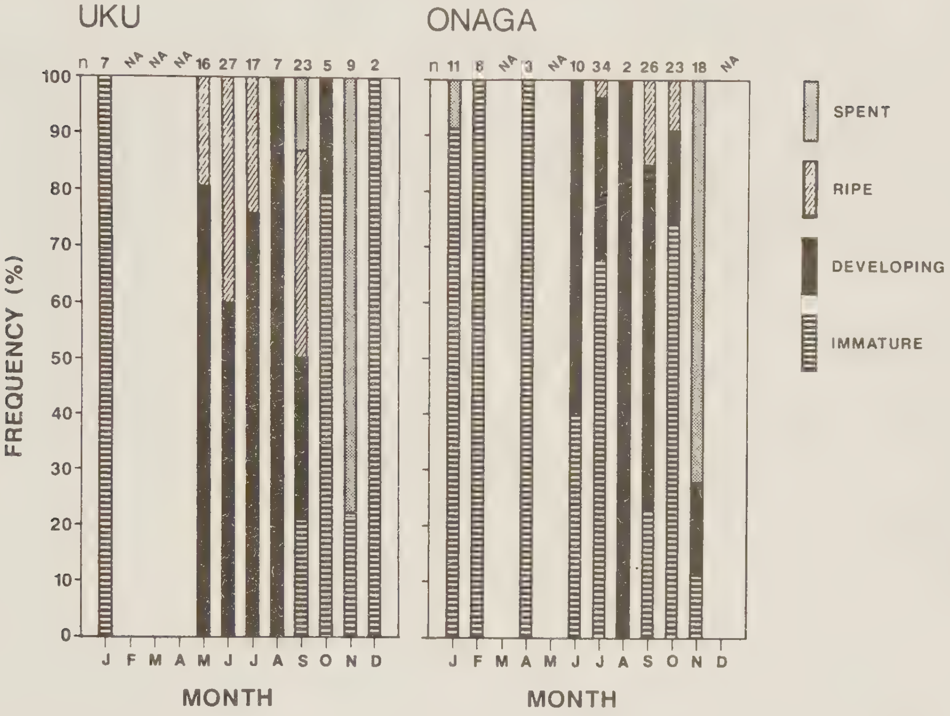


FIGURE 4.—Monthly percentages of uku and onaga ovaries at various stages of development determined by visual staging methods. N = number of samples per month.

500 mm size class, 100% were mature. The smallest uku with vitellogenic (stage II) ovaries during the spawning season was 429 mm FL (1.27 kg), which is 41.7% of the maximum length (MAXLEN) recorded for the study animals. The smallest individual with ripe (stage III) ovaries was 477 mm FL (1.82 kg) or 46.4% of the MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL (Fig. 6) was 449 mm FL ($a = -0.3444$, $b =$

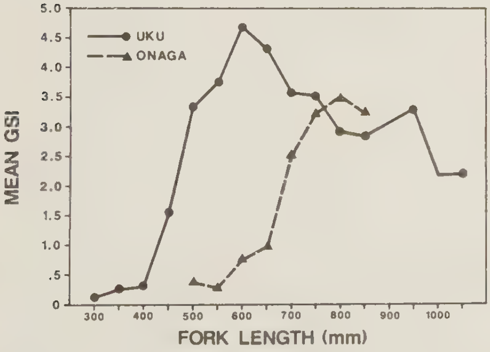


FIGURE 5.—Mean gonosomatic index (GSI) plotted by 50 mm FL intervals for female uku and onaga sampled during their respective spawning seasons.

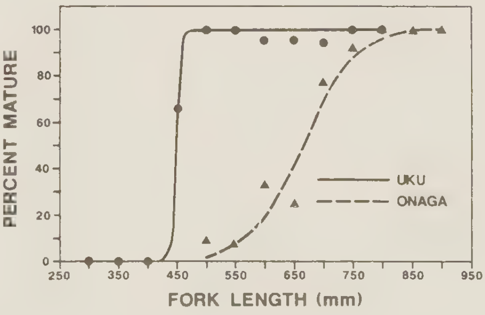


FIGURE 6.—Proportion of sexually mature female uku and onaga within each size class, plotted with the predicted proportion of mature females.

154.31). Interesting to note was the propensity for decreasing mean GSI's in uku larger than 600 mm FL (Fig. 5).

In contrast, the smallest mature onaga was 522 mm FL (2.22 kg) or 53.9% MAXLEN, and ripe individuals were not encountered until 605 mm FL (3.22 kg) or 62.4% MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL was 663 mm FL ($a = -0.0233$, $b = 15.462$; Fig. 6), and 77% of the onaga in the 675–725 mm FL class were found to be at stage II of development or beyond (Table 2). Onaga spawned over a narrower size range (600–900 mm FL; Fig. 5) compared with uku (450–1,050 mm FL; Fig. 5).

Histological examination of ovaries indicated that both species follow a similar pattern of development (Fig. 7). The progression from oogonia to hydration is typical of snappers and has been covered in detail by Crossland (1977) and Wallace and Selman (1981). Postovulatory follicles were not identifiable in tissue sections from ripe (stage III) ovaries of either species. None of the immature (stage I) ovaries examined histologically showed signs of atresia, indicating that these fish had not previously spawned. Identifiably atretic individuals in later stages of development were not observed until the end of the spawning season.

Spawning Frequency and Pattern of Egg Release

The size-frequency distributions of oocyte diameter were constructed for ovaries of uku caught during the spawning season, using the volumetric method, and were found to be polymodal, suggesting that uku may release multiple egg batches (Fig. 8a). All ovaries possessed a

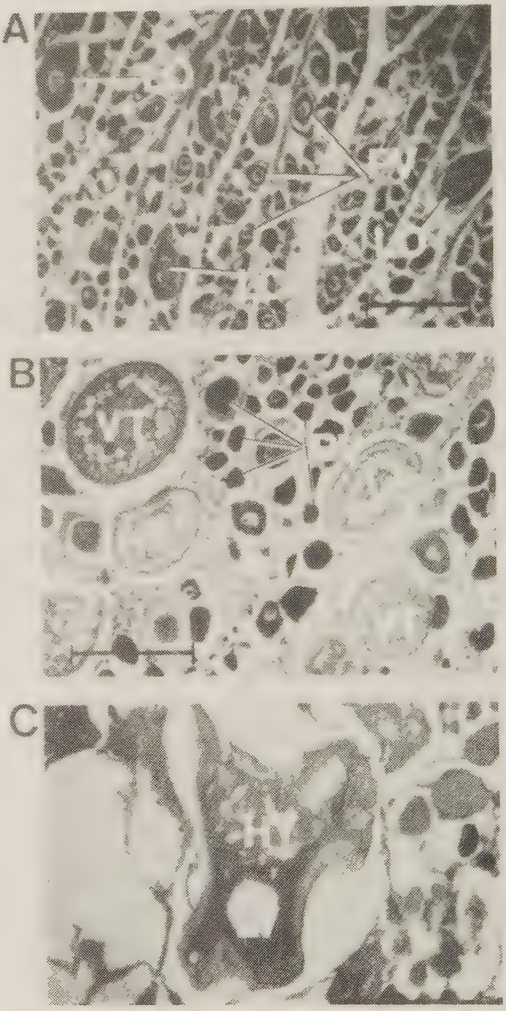
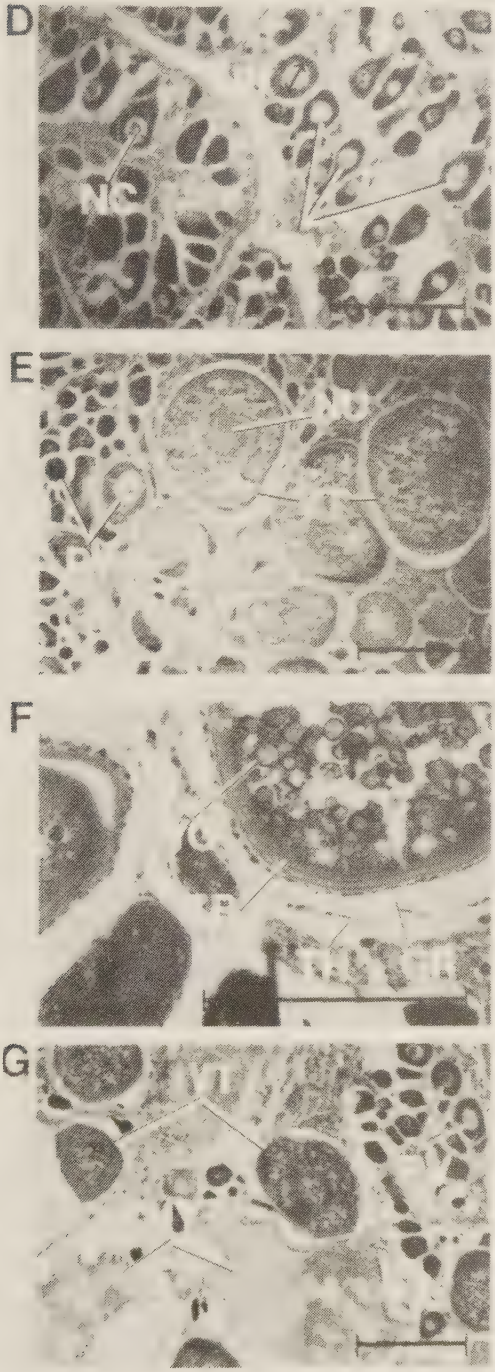


FIGURE 7.—Photomicrographs showing transverse histological sections of uku and onaga ovaries in various stages of development. Scale bars represent 0.10 mm. A. Early developing uku (386 mm FL) ovary classified as juvenile (stage I) containing numerous previtellogenic (PV) oocytes. Larger oocytes (LO) have reached the lipoid or yolk vesicle stage, just prior to vitellogenesis. B. Developing (stage II) uku (525 mm FL) ovary. Shown are previtellogenic (PV) and vitellogenic (VT) oocytes. C. Ripe (stage III) uku (541 mm FL) ovary with hydrated (HY) oocytes. Lipoid vesicles have fused to form a single mass (LV). D. Juvenile (stage I) onaga (506 mm FL) ovary consisting of previtellogenic (PV) oocytes with large central nucleus (NU) containing numerous nucleoli (NC). E. Developing (stage II) onaga (753 mm FL) ovary showing numerous mature oocytes in different stages of vitellogenesis (VT). F. Enlargement of a developing onaga ovary. Shown are granulosa (GR) and thecal (TH) cell layers, zona radiata (ZR), and yolk granules (YG). G. Ripe (stage III) onaga (605 mm FL) ovary showing hydrated (HY), vitellogenic (VT) and previtellogenic (PV) oocytes.



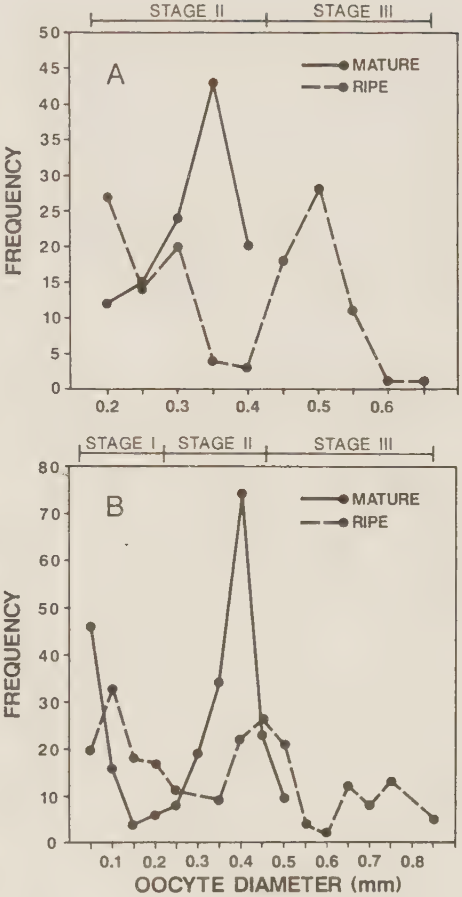


FIGURE 8.—Size-frequency distributions of uku ovaries in various stages of development (cf. Table 1) preserved in (A) Gilson's fluid and (B) Bouin's fluid. Each distribution shown represents a single ovary.

mode of immature oocytes not represented in the figure. Stage II ovaries contained a mode of oocytes at 0.30–0.35 mm, representing various stages of vitellogenesis, while stage III ovaries included this developing mode and another mode (0.50 mm) nearing hydration. A large amount of variation was noted in the relative frequency of oocytes in the most advanced mode of the stage III ovaries. Similar results were exhibited for size-frequency distributions of uku ovaries constructed by the cork borer method. This method allowed delineation of the immature mode as well as the other advanced stages (Fig. 8b). Additional evidence that multiple batches of oocytes ripen and are successively spawned was indicated by the wide range in GSI values calculated for both species during the spawning season.

Sex Ratio

The sex ratio of male to female uku was 1.05:1 (51.2% males, $N = 559$ individuals combined). A chi-square goodness of fit test suggested that this ratio was not significantly different from the expected 1:1 ratio ($\chi^2 = 0.302$, $P > 0.05$). By examining sex ratio at 50 mm FL intervals, independence was determined and the percentage of females was shown to decrease between the 600 and 750 mm FL categories from 50.0 to 40.9%, then increase 65.5% at 800 mm FL before reaching 100% beyond 900 mm FL. Based on two-way contingency table analysis, the percentage of females caught increased significantly towards the end of the spawning season (September–October; Table 3). Males were caught in higher percentages in the spawning months from May to July.

The sex ratio of male to female onaga differed significantly ($\chi^2 = 8.99$, $P < 0.05$) from 1:1 in favor of males (61.4%, $N = 347$ individuals combined). The overall ratio of males to females was 1.59:1. There was a significant preponderance of males within the 50 mm FL intervals from 600 to 750 mm. However, females predominated above 850 mm FL, reaching 100% of the individuals in the 950 mm FL category. The two-way contingency table analysis suggested that sex and month of capture were not independent (Table 3).

TABLE 3.—Tests of the hypothesis that sex ratio of uku and onaga did not vary significantly from the sample populations during the year. Data are pooled by 2 mo intervals for samples collected in 1984–87 (df = 5).

	Uku			Onaga		
Month	N	Percentage female	Contribution to total χ^2	N	Percentage female	Contribution to total χ^2
Jan.–Feb.	15 } 17			56	37.5	0.277
Mar.–Apr.	2	47.0	0.027	19	15.8	4.976
May–June	359	46.5	0.776	23	60.9	3.771
July–Aug.	88	43.0	1.637	76	47.4	1.292
Sept.–Oct.	69	63.8	6.153	130	33.9	2.719
Nov.–Dec.	28	64.3	2.673	62	41.9	0.174
Total			11.266*			13.209*

* = $P < 0.05$.

DISCUSSION

The spawning season for both uku and onaga extends throughout the summer months in Hawaii, as evidenced by the advanced condition of the ovaries and the peaks in ova diameters and GSI values during this period. This pattern has been reported in Hawaii for other snapper species, including *E. carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984). Spawning activity also occurs during the austral summer for populations of *A. virescens* from New Caledonia (Fourmanoir and Laboute 1976) and East Africa (Talbot 1960; Nzioka 1979). Likewise, peak summer spawning with intermittent activity throughout the rest of the year seemed to be the pattern for *E. coruscans* in Vanuatu (Brouard and Grandperrin 1985). The seasonal peak in spawning activity may be most closely tied to increases in water temperature and day length, as suggested by Walsh (1987) who observed that spawning activity for Hawaiian reef fishes declined rapidly in September to October as maximum water temperatures were reached. This pattern would ensure optimum temperature conditions for developing larvae. A similar post-summer spawning decline associated with changing local environmental conditions was noted by Grimes and Huntsman (1980) for *Rhomboplites aurorubens* from North and South Carolina and by Everson (1984) for *E. carbunculus*. The extension of onaga's spawning season into November, with a peak in October, may reflect that the genus *Etelis* is restricted to much greater depths than are the other reef-associated lutjanid species. Seasonal changes in temperature and photoperiod are much less pronounced at these depths. In Vanuatu, Brouard and Grandperrin (1985) found that seasonal changes in gonad maturation based on GSI values differed among species inhabiting discrete depths.

Grimes (1987) has suggested two distinct spawning patterns for snappers. One is a restricted pattern with spawning centered around the summer months, typical of species associated with continental habitats where peaks in production cycles occur because of nutrient run-off resulting from high rainfall. The opposing pattern is characterized by year-round spawning with peaks occurring in spring and fall, a pattern thought to be typical of less productive insular populations. Grimes (1987) has noted that Cuba and New Caledonia are large islands that follow the continental pattern, with spawning peaks arising during periods of high rainfall. *Etelis carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984) have also been reported to follow a restricted spawning pattern in the Northwestern Hawaiian Islands. Both uku and onaga in our study also followed the restricted spawning pattern associated with continental habitats. Spawning took place over a protracted period centered around the summer months. Neither species was found in spawning condition at any other time of the year. Since temporal primary production cycles exhibit little seasonal variation throughout the Hawaiian Archipelago (Bienfang and Szyper 1981; Bienfang et al. 1984), the basis for this restricted pattern observed for uku and onaga is unclear. Apparently, the seasonal changes in day length and water temperature in Hawaii provide adequate spawning stimuli.

Interspecies differences in size at sexual maturity also were noted. The slope of the logistic curve fitted to the size at sexual maturity data was considerably steeper for uku compared with onaga (Fig. 6). Uku matured at 450–500 mm FL, with nearly 100% mature above 550 mm FL, and onaga matured at 550–800 mm FL, with 100% mature at 850 mm FL. Size at sexual maturity differed between species in terms of the percentage of MAXLEN at which maturity occurred. Uku began maturing at about 429 mm FL or 42% of their MAXLEN, whereas onaga began maturing at about 522 mm FL or 54% of their MAXLEN. Talbot (1960) reported that male and female *A. virescens* of East Africa reached maturity at 410 mm SL (51%) and 465 mm SL (58%), respectively. *Aprion virescens* off Vanuatu matured at 440 mm FL, a figure that Brouard and Grandperrin (1985) calculated from a MAXLEN coefficient of 57.6%, which was based upon the average values obtained from 34 tropical fish species from the west coast of Africa. The same coefficient, applied to Vanuatu populations of *E. coruscans*, indicated that sexual maturity was reached at 470 mm FL, although developmental staging data obtained for this species revealed that mature fish were first sampled at 330–380 mm FL. The actual size at which maturity commenced in all of these locations agreed closely with our data for uku in Hawaii, while the percentage of MAXLEN values differed considerably. However, Hawaii and Vanuatu populations of onaga matured at substantially different sizes.

Disparities in size at sexual maturity between areas may reflect differences in resource utilization and growth allocation. Grimes (1987) calculated the average percentage of MAXLEN at which sexual maturity occurred for lutjanid populations occupying similar zoogeographic locations and habitats. Insular and continental populations had average MAXLEN values of 51 and 43%, respectively, while the deep (> 91 m) and shallow (< 91 m) species were calculated at 49 and 43%. The MAXLEN value of 42% calculated for the study population of uku indicates that this species fits the shallow, continental pattern. As previously mentioned, onaga are found at much greater depths and therefore seem to be less influenced by continental effects than uku. These observations are substantiated by the fact that the MAXLEN value of 54% calculated for onaga conforms closest to the deep, insular pattern reported in Grimes (1987). He reasoned that these anomalies may result from regional differences in food production. Fish from a relatively resource-rich environment may mature at a proportionally smaller size than fish in less productive habitats. He further speculated that selection may favor maturation at a larger maturing size in insular regions because the cost of year-round spawning may be higher in these areas.

Estimates of von Bertalanffy growth parameters, derived from weight-frequency distributions for uku and onaga landed in Hawaii in 1984–86, indicate that uku mature at about ages 4–5 (429 mm FL), while onaga begin maturing at ages 5–6 (522 mm FL) (Ralston and Kawamoto, fn. 1). In the same study, Ralston and Kawamoto (fn. 1) calculated the size at entry to the fishery as 650 mm FL for uku and 450 mm FL for onaga in the main Hawaiian Islands, indicating that, for onaga, the present fishery is capturing individuals that have not yet reached sexual maturity. Continuing this practice could lead to a serious decline in spawning stock biomass (Polovina 1987).

Sex ratio also differed between the two species. The ratio of male to female uku was judged not significantly different from the expected ratio of 1:1. In contrast, the onaga sex ratio was significantly different from unity in favor of males. Females dominated in the larger size classes for both species. The preponderance of large females has also been reported for other snapper species, including *Lutjanus synagris* (Reshetnikov and Claro 1976), *R. aurorubens* (Grimes and Huntsman 1980), and *E. carbunculus* (Everson 1984). This phenomenon is thought to be due to differential mortality of the sexes rather than to growth (Wenner 1972; Grimes and Huntsman 1980). The preponderance of male onaga in the smaller size ranges is more difficult to explain and may reflect intersexual behavioral differences. If smaller males feed more aggressively, they would be overly abundant in the catch. Differences in feeding behavior may also explain monthly variations in sex ratio reported for both species. The ratio of female uku increased markedly at the close of the spawning season, suggesting a heightened vulnerability to the fishing gear owing to what may be greater nutritional demands of postspawning females. Seasonally, the largest catch of uku occurs in summer (May–October), when fish are thought to form spawning aggregations (Ralston, fn. 2).

Numerous investigators have suggested that snappers are multiple spawners, based upon the presence of multiple size modes of developing oocytes (Min et al. 1977; Grimes and Huntsman 1980; Everson 1984; Kikkawa 1984; Grimes 1987). Other evidence reported as substantiating this phenomenon has been the wide variations exhibited in GSI's of *L. griseus* (Starck and Schroeder 1970) and *R. aurorubens* (Grimes and Huntsman 1980) during the spawning season. Ralston (1981) suggested that *P. filamentosus* is a multiple spawner because the ovaries of ripe females make up only about 4% of the total body weight, a relatively small percentage compared with that of a single spawning temperate species. These observations, the presence of multiple size modes of developing oocytes and the wide variations in GSI's, were noted for uku and onaga and suggested that these species also spawn repeatedly during the spawning season. Although it has been documented that the oocyte size-frequency distribution of many snapper species contains two or three distinct modes, the exact number of batches spawned per season is rarely reported. This is because the process of recruitment from the undifferentiated oocyte pool is dynamic and difficult to characterize (Grimes 1987).

Much of the above evidence is largely contingent on the assumption that multiple oocyte modes continue to develop and are successively spawned. Foucher and Beamish (1980) observed that, for Pacific hake, *Merluccius productus*, from the Strait of Georgia, oocyte development was multimodal during the spawning season, suggesting multiple spawning for this species. Histological examination of the ovaries revealed, however, that only the largest batch became hydrated and was spawned and all remaining residual yolked oocytes were resorbed. More direct evidence for this mode of spawning, as well as the delineation of the number of batches spawned, has been obtained through the process of identifying and ageing postovulatory follicles in species that exhibit these multiple modes of oocyte development. This method has been used to estimate spawning frequency in several engraulid species (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985; Alheit et al. 1984; Parrish et al. 1986; Clarke 1987) and also for the skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986). Ageing postovulatory follicles seems to work well for species normally found in large aggregations or schools but has yet to be applied to snappers. The ageing method using postovulatory follicles may be more difficult to apply to such species as snappers, which are known to occur in fewer numbers. Although our study attempted to identify postovulatory follicles in natural populations of uku and onaga, they could not be positively identified or aged. Future studies will have to address this problem, since the delineation of spawning frequency is important for accurate fecundity estimates.

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LITERATURE CITED

Alheit, J., V. H. Alarcon, and B. J. Macewicz.
1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. Calif. Coop. Oceanic Fish. Invest. Rep. 25, p. 43–52.

Allen, G. R.
1985. FAO species catalogue. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 125, Vol. 6, 208 p. + colored plates.

Amesbury, S. S., and R. F. Myers.
1982. Guide to the coastal resources of Guam, volume I. The fishes. Univ. Guam Mar. Lab. Contrib. 173, 141 p.

Bagenal, T. B., and E. Braum.
1968. Eggs and early life history. *In* W. E. Ricker (editor), IBP handbook No. 3, methods for assessment of fish production in fresh waters, p. 159–181. Blackwell Scientific Publ., Oxford and Edinburgh.

Bienfang, P. K., and J. P. Szyper.
1981. Phytoplankton dynamics in the subtropical Pacific Ocean off Hawaii. Deep-Sea Res. 28A(9): 981–1000.

Bienfang, P. K., J. P. Szyper, M. Y. Okamoto, and E. K. Noda.
1984. Temporal and spatial variability of phytoplankton in a subtropical ecosystem. Limnol. Oceanogr. 29:527–539.

Brouard, F., and R. Grandperrin.
1985. Deep-bottom fishes of the outer reef slope in Vanuatu. South Pacific Commission, Seventeenth Regional Technical Meeting on Fisheries, Noumea, New Caledonia, 5–9 August 1985. SPC/Fisheries 17/WP.12, 126 p.

Clarke, T. A.
1987. Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85:127–138.

Crossland, J.
1977. Seasonal reproductive cycle of snapper *Chrysophrys auratus* (Forster) in the Hauraki Gulf. N.Z. J. Mar. Freshwater Res. 11:37–60.

Druzhinin, A. D.
1970. The range and biology of snappers (Fam. Lutjanidae). J. Ichthyol. 10:717–736.

Everson, A. R.
1984. Spawning and gonadal maturation of the ehu, *Etelis carbunculus*, in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 128–148. UNIHI-SEAGRANT-MR-84-01.

Foucher, R. P., and R. J. Beamish.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41–48.

Fourmanoir, P., and P. Laboute.
1976. Poissons de Nouvelle-Calédonie et des Nouvelles Hébrides. Les éditions du Pacifique, Papeete, Tahiti, 376 p.

Grimes, C. B.
1987. Reproductive biology of the Lutjanidae: A review. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 239–294. Westview Press, Boulder.

Grimes, C. B., and G. R. Huntsman.
1980. Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina. Fish. Bull., U.S. 78:137–146.

Gunderson, D. R., P. Callahan, and B. Goiney.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4): 74–79.

Hilge, V.
1977. On the determination of the stages of gonad ripeness in female bony fishes. Meeresforchung 25(1976/77):149–155.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 77:641–652.

Hunter, J. R., and B. J. Macewicz.
1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax*, during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21:139–149.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (editor), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 79–94. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert.
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull., U.S. 84:895–903.

Kikkawa, B. S.
1984. Maturation, spawning, and fecundity of opakapaka, *Pristipomoides filamentosus*, in the Northwestern Hawaiian Islands. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 149–160. UNIHI-SEAGRANT-MR-84-01.

Kikkawa, B. S., and A. R. Everson.
1984. Gonadal maturation, fecundity, and spawning of the greater amberjack, *Seriola dumerili* (Risso), in Hawaiian waters with references to ciguatoxin incidences. *In* R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands,

Vol. 2, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii, p. 161–178. UNIHI-SEAGRANT-MR-84-01.

Masuda, H., C. Araga, and T. Yoshino.
1975. Coastal fishes of southern Japan. [In Jpn.] Tokai Univ. Press, Tokyo, 379 p.

Min, T. S., T. Senta, and S. Supongpan.
1977. Fisheries biology of *Pristipomoides* spp. (Family Lutjanidae) in the South China Sea and its adjacent waters. Singapore J. Primary Ind. 5(2):96–115.

Ni, I-H., and E. J. Sandeman.
1984. Size at maturity for northwest Atlantic redfishes (*Sebastes*). Can. J. Fish. Aquat. Sci. 41:1753–1762.

Nzioka, R. M.
1979. Observations on the spawning seasons of East African reef fishes. J. Fish Biol. 14:329–342.

Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil.
1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 84:503–517.

Polovina, J. J.
1987. Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 505–532. Westview Press, Boulder.

Pooley, S. G.
1987. Demand considerations in fisheries management—Hawaii's market for bottom fish. *In* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 605–638. Westview Press, Boulder.

Ralston, S.
1981. A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Ph.D. Thesis, Univ. Washington, Seattle, 204 p.

Reshetnikov, Yu. S., and R. M. Claro.
1976. Cycles of biological processes in tropical fishes with reference to *Lutjanus synagris*. J. Ichthyol. 16:711–723.

Snedecor, G. W., and W. G. Cochran.
1978. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, IA, 593 p.

Starck, W. A., II, and R. E. Schroeder.
1970. Investigations on the gray snapper, *Lutjanus griseus*. Stud. Trop. Oceanogr. (Miami) 10, 224 p. (Copyright 1971).

Talbot, F. H.
1960. Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskal). Ann. S. Afr. Mus. 45:549–573.

Van Dalsen, A. P.
1977. An improved technique for subsampling eggs for fecundity studies. Fish. Bull., S. Afr. 9:6–10.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Walsh, W. J.
1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fishes 18:257–276.

Wenner, A. M.
1972. Sex ratio as a fuction of size in marine crustacea. Am. Nat. 106:321–350.

Western Pacific Regional Fishery Management Council.
1986. Combined fishery management plan, environmental assessment and regulatory impact review for the bottomfish and seamount groundfish fisheries of the western Pacific region. Western Pacific Regional Fishery Management Council, 1164 Bishop Street, Honolulu, HI 96813, var. pag.

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Variability of the Columbia River plume observed in visible and infrared satellite imagery

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Abstract. Variability of the Columbia River plume in coastal waters off the northwestern United States, 1979–1985, was observed in sea surface temperature and phytoplankton pigment images derived from Advanced Very High Resolution Radiometer and Coastal Zone Colour Scanner data. The orientation, shape, intensity and relative temperature of the plume vary in response to coastal winds and wind-driven surface currents. From October to April, plume water is oriented northward along the coast. Following the spring transition in April or May, the plume is oriented southward, either adjacent to the coast or offshore. Transition between the winter and summer forms can be observed in the satellite imagery. Brief reversals of the prevailing seasonal winds cause rapid changes in the orientation and shape of the plume. Remote sensing of the Columbia River plume offers valuable information for oceanographic studies and fisheries management in the region. Derivation of an appropriate visible–infrared signature for plume waters and tracking of tidal pulses in the plume is suggested as a promising direction for future research.

1. Introduction

The Columbia River, with a mean flow of $7300\,\mathrm{m^3\,s^{-1}}$, is the largest point source of freshwater flow into the eastern Pacific Ocean. Columbia River water forms a low-salinity plume extending outward from the river mouth above a shallow (<20 m) halocline. Seawater is entrained into this plume by wind-generated turbulence and by frontal mixing and secondary lateral flow induced by potential energy within the plume (McClimans 1979). River flow and turbulent mixing rates are such that anomalously low surface salinities ($<32{\cdot}5$ psu) may be detected over the entire shelf and slope and out to 400 km from the coast of Washington and Oregon (figure 1).

The Columbia River estuary is partially mixed, meaning that seawater intrudes beneath the freshwater outflow, except at very high or low stages of river flow (Neal 1972). A recent model study of such estuaries (Zhang *et al.* 1987) has shown that the basic tendency of a river plume to turn to the right, facing downstream in the northern hemisphere, is modified and even reversed by the steepness of the continental shelf and by longshore surface current velocity. The Columbia River plume flows out over a relatively narrow and steep shelf, accentuating the Coriolis deflection, but is subject to strong seasonal variation in longshore flow of coastal waters.

Coastal surface currents in this region are primarily wind-driven (Huyer *et al.* 1975, Huyer 1979, Hickey 1979 a). Seasonal variability is very strong: large-scale changes in atmospheric pressure systems over the North Pacific drive spring and fall transitions in prevailing winds, sea level, currents, and temperature on the continental

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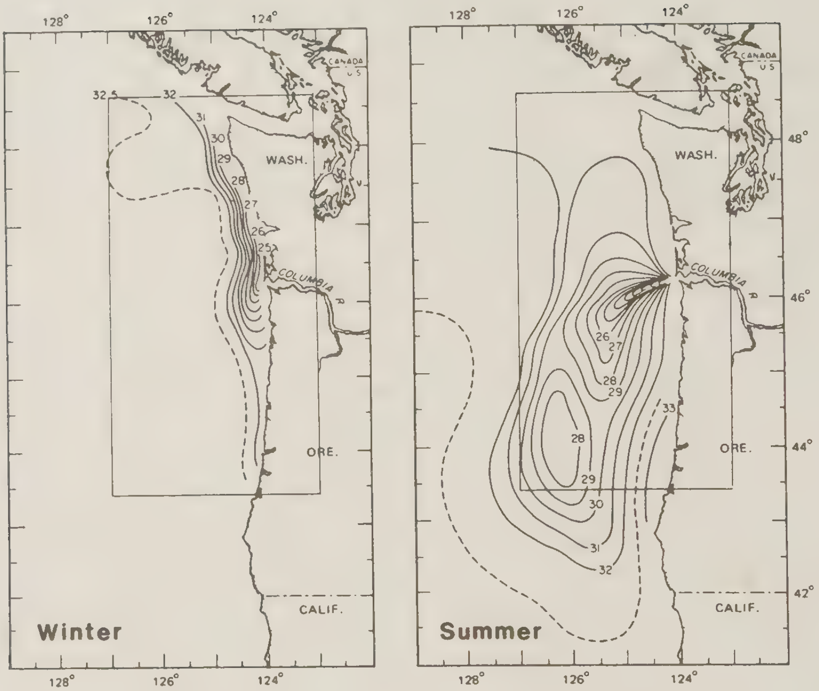

Figure 1. Generalized winter and summer surface salinity distributions in the Columbia River plume region (Barnes *et al.* 1979, figure 3.12). Box indicates coverage of satellite imagery in figures 4, 5, and 6.

shelf (Strub *et al.* 1987 a,b). In winter, southerly winds cause onshore Ekman transport of surface water, high sea level and downwelling of isopycnal surfaces towards the coast. These conditions are balanced by northward geostrophic flow. As prevailing winds shift from southerly to northerly in April–May, offshore Ekman transport begins, sea level drops, and upwelling causes isopycnal surfaces to slope upwards towards the coast. The resulting geostrophic flow is then southward. Surface temperatures decline as summer upwelling intensifies. The fall transition back to winter downwelling, high sea level and northward surface currents occurs in September–October.

Seasonal variability in the distribution of plume water is known from conventional hydrographic surveys (Barnes *et al.* 1972). In general, the plume is oriented northward in winter and southward in summer, transported by alongshore surface currents. Repetitive point sampling from ships has indicated that the plume responds quickly to high-frequency (days) changes in local winds (Hickey 1979 b). The size of the plume may be affected by Columbia River flow, which varies by a factor of five or more over the year, with a maximum in May–June from snowmelt and a minimum in late summer (Barnes *et al.* 1972). However, we will consider variations in surface winds and wind-driven currents as the primary cause of variability of the Columbia River plume.

Variability on seasonal and shorter time scales can be monitored effectively with satellite sensors covering large areas synoptically, with a resolution of ~1 km. Under good viewing conditions, the plume is clearly defined by its visible and infrared signature. The apparent phytoplankton pigment concentration of plume water, measured by the Coastal Zone Colour Scanner (CZCS), is very high. Its surface temperature, measured by the Advanced Very High Resolution Radiometer (AVHRR), is colder than surrounding coastal ocean water in winter and warmer in summer.

We examined the variability of the Columbia River plume as part of a study of survival of juvenile salmon released from Columbia River hatcheries. The goal of the larger study is to use satellite imagery and other real-time environmental data to optimize the timing of hatchery releases for maximum survival. We describe the plume variability results here as an illustration of the use of satellite imagery in studying and monitoring an important aspect of the coastal ocean in the northeast Pacific.

2. Methods

Satellite data were processed at the Scripps Satellite Oceanography Facility of the Scripps Institute of Oceanography in La Jolla, California. Image data were examined primarily from April–July for 1979–1985, because of the scope of the juvenile salmon survival study. For 1982, we processed a monthly time series of imagery to cover the entire annual cycle.

Daytime thermal infrared data, from channel 4 (11 μm) of the AVHRR (on NOAA-6 and NOAA-7 satellites), were corrected for the effect of thin low clouds using channel 2 (0·7 μm–1·1 μm) near-infrared data (Gower 1985). Infrared radiance was then converted to brightness temperature following Lauritson *et al.* (1979).

Visible radiances from the CZCS (operational on the Nimbus-7 satellite from August 1978 to June 1986), were processed with an algorithm based on Gordon *et al.* (1983) to remove effects of Rayleigh and aerosol scattering and to compute pigment concentrations from corrected blue:green radiance ratios. AVHRR and CZCS images were co-registered to a Mercator grid covering the coast of Washington and Oregon.

CZCS pigment algorithms are appropriate for estimating phytoplankton pigment concentration only in Case 1 waters, where photoplankton cells and associated products are the only important determinants of optical properties (Gordon and Morel 1983). River plumes are Case 2 waters, containing terrigenous sediments and dissolved organic matter, as well as anthropogenic material. The 'apparent' pigment concentration derived by the CZCS algorithm is used here as a qualitative index of the green:blue colour signature of plume water, rather than as an estimate of phytoplankton pigment concentration. Any additional error in this estimate caused by using a single-scattering approximation to compute the Rayleigh scattering radiance (Gordon *et al.* 1988) does not affect its use as a colour-signature index.

The 1979–1985 coastal wind velocity and surface wind stress, in a three-degree square centred at 46° N 124·5° W (55 km SW of the river mouth), were computed at 6 h intervals from U.S. Navy Fleet Numerical Oceanography Center surface pressure analyses by the NMFS/Pacific Fisheries Environmental Group in Monterey, California (see Bakun (1975) for methodology). A smoothed time series of 12 h mean wind vectors (five-point running mean, weighted 1:2:3:2:1) is presented here.

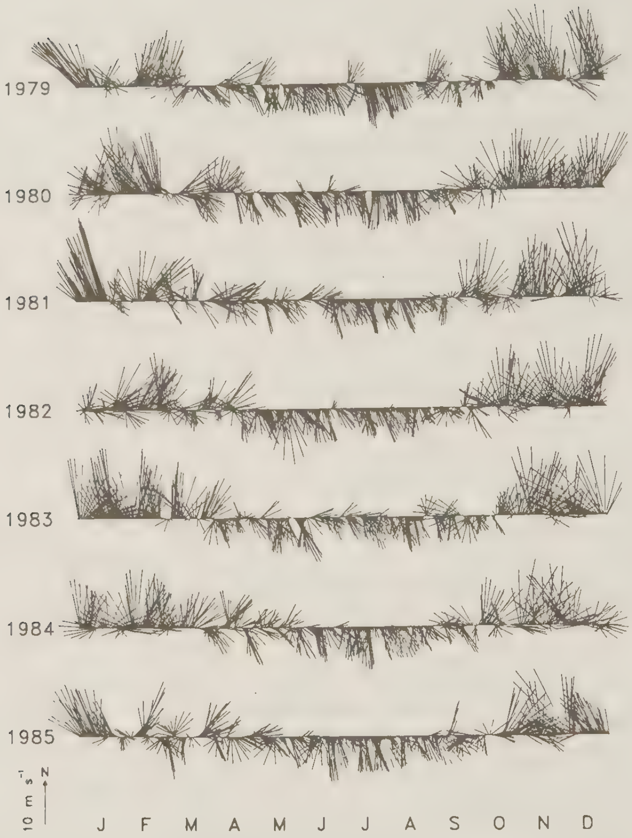

Figure 2. Time series of calculated wind vectors (smoothed 12 h means) at 46° N 124·5° W.

3. Results and discussion

3.1. *Winds*

The wind velocity time series (figure 2) shows strong seasonality, with northerly winds prevailing from May through September and strong southerly winds from October through April. The spring transition is marked by a change from prevailing southerly to northerly winds. The timing of the spring transition varies from year to year, with nominal dates as follows: 8 May 1979, 20 April 1980, 23 June 1981, 22 April 1982, 4 April 1983, 26 May 1984 and 5 May 1985.

Higher-frequency fluctuations in wind velocity, at the scale of about a week, appear as occasional relaxations or reversals of the seasonal prevailing winds. These fluctuations are caused by the passage of storm systems through the area.

3.2. *Plume*

Satellite images found to provide adequate coverage of the Columbia River plume and processed to yield sea surface temperature (AVHRR) or colour (CZCS) fields are listed in the table. Orientation, shape, size, intensity and relative temperature of the

Satellite imagery of the Columbia River plume region. Image data types: T = sea surface temperature from AVHRR, P = phytoplankton pigments from CZCS. Description includes: (1) orientations of major axis and secondary flows (for N or S major axis, onshore = adjacent to coast, offshore = separated from coast by coastal water); (2) shape, when well defined: round = relatively circular, short = elongated and less than twice as long as wide, long = elongated and more than twice as long as wide; (3) Front = intense temperature and/or colour front near the mouth at edges of the plume off the major axis, and (4) Temperature relative to surrounding coastal water (warm or cold).

Date	Type	Plume description
1979, 19 May	P	SSW, long, front
21 May	P	SSW then WSW, long
30 May	P	SW, short, front
14 July	P	W then N, short, front
1980, 10, 11 April	P,T,	N onshore, short, cold
21 April	P	N onshore, some S
26 April	P	W, some N, round, front
17 May	P	SSW, short, front
30 June	P	SSW, short, front
6 July	T,P	SW then N onshore, short, cold
1981, 28 May	P	W, some N, round
10, 13 June	T,P	W, some S, round, front, warm
2 July	T,P	W then SSW, long, warm
1982, 5 February	T,P	N, round, front, cold
21 March	T,P	W then N, long, cold
21 April	P	W, short
24, 25 April	T,P	WSW, short, front, warm
24 May	T,P	SSW, long, front, warm
28 May	T,P	S onshore, long, front, warm
12 July	T,P	WSW, round, warm
17, 18 August	T,P	SW, long, warm
23 September	T,P	W, short, warm
30 September	T,P	W then N, warm
12, 13 October	P,T	W then N, not well defined
9, 10 November	P,T	N onshore, front, cold
1983, 13 April	P	W, some S, round, front
15 April	T,P	W then S, short, front, cold
16 April	P	SW, short, front
12 May	T,P	W then N and W, some S, short, cold
22 May	T,P	S offshore then W, long, warm
20 June	T,	S onshore, short, front, warm
15 September	T,P	SW, short, warm
1984, 14 July	T	SW, long, warm
16 July	T	W then SSW, long, front, warm
20, 21 August	T,P	W then S, short, front, warm
1985, 7 May	T,P	N, round, some S, front, warm
15 May	T,P	SSW then W, long, warm
9 June	T	W, round, front, warm
17, 18 June	T,P	S offshore when W, long, front, warm

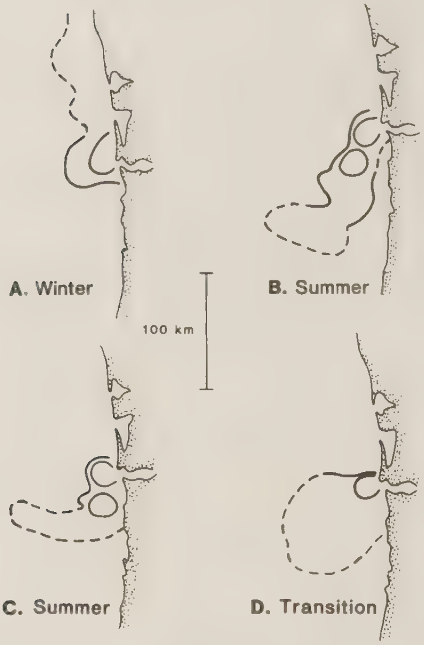

Figure 3. Schematic drawings of basic forms of the Columbia River plume. Solid lines represent strong colour and/or temperature boundaries, dashed lines represent weaker boundaries.

plume vary in these images. A seasonal pattern of two basic forms is illustrated schematically in figure 3.

During winter, plume water is advected northward along the coast (figure 3 (*a*)). The most obvious plume water is a semi-circular mass of green water, colder than the surrounding coastal water, just north of the mouth. Water along the coast north of this mass is still relatively cold and green, but is probably a mixture of Columbia River water, run-off from coastal rivers and oceanic surface water driven onshore.

During summer, the plume is advected southward, usually separated from the coast (figure 3 (*b*)) due to offshore Ekman transport, but sometimes adjacent to it (figure 3 (*c*)). Plume water is warmer than surrounding coastal water, which is cooled by upwelling. During transition between the basic winter and summer forms, the plume is roughly circular at the mouth of the river (figure 3 (*d*)).

Details of the plume's variable characteristics are briefly described in the table. These details will be discussed in the following descriptions of the plume's responses to winds and other forcing.

3.3. *Spring transition*

A sequence of CZCS images from 1982 (figure 4) illustrates a typical spring transition. On 2 February, the plume is in the typical winter form, advected to the north along the coast. Intermittent northerly winds during 4–24 March forced the plume offshore by 21 March. Northerly wind events also occurred on 6–10 April and

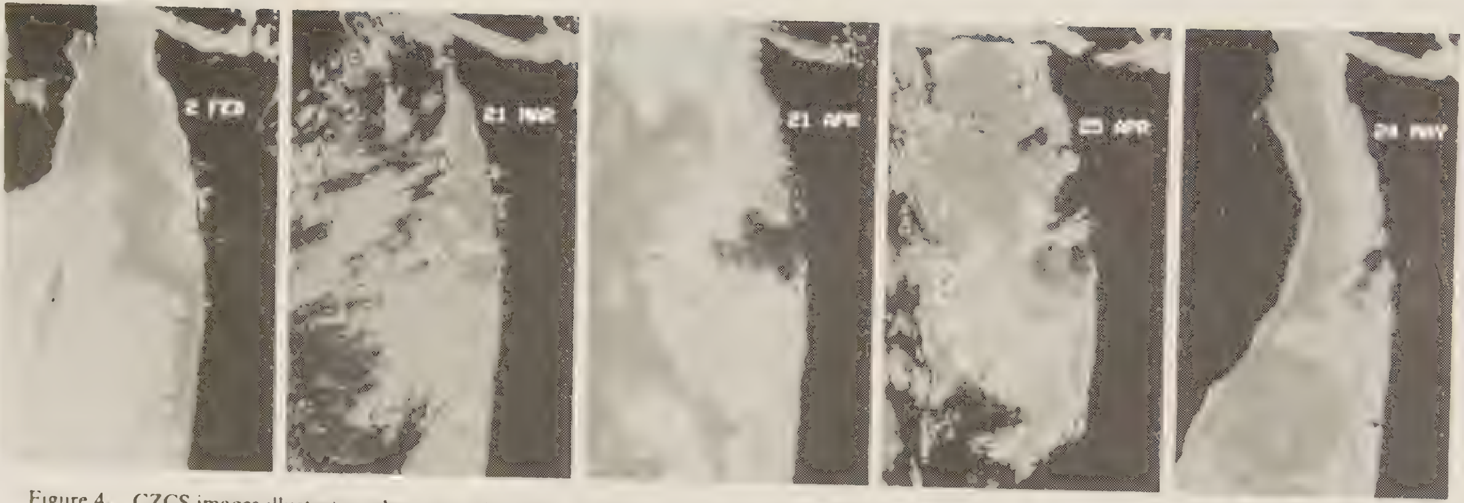

Figure 4. CZCS images illustrating changes in the Columbia River plume during spring transition in 1982. Colours indicate increasing phytoplankton pigment concentrations: purples ($<0{\cdot}1\,\mathrm{mg\,m^{-3}}$), blues ($0{\cdot}1$–$0{\cdot}4\,\mathrm{mg\,m^{-3}}$), greens ($0{\cdot}4$–$1{\cdot}5\,\mathrm{mg\,m^{-3}}$), yellow and oranges ($1{\cdot}5$–$4{\cdot}0\,\mathrm{mg\,m^{-3}}$), reds ($>4{\cdot}0\,\mathrm{mg\,m^{-3}}$).

17–20 April, although prevailing northerly winds did not begin until 23 April, the nominal date of the spring transition. Thus, on 21 April, the plume is in transition, roughly circular and oriented W of the river mouth. On 25 April, the plume is still in transition, but now oriented WSW. On 24 May, after a month of prevailing summer northerlies, the plume is in the typical summer form, elongated and oriented SWS.

A rapid spring transition is seen in two images from 1985 (not shown here). The nominal date of spring transition was 14 May, although intermittent northerly winds occurred during 4–12 May. A CZCS image on 7 May shows the plume in a winter form, but beginning transition: most of the green plume water is along the coast to the north of the river mouth, but there appears to be some flow to the south. The next available image on 15 May shows the plume in a well developed summer form, elongated and oriented WSW.

These observations show that the spring transition of the plume may be initiated by intermittent northerly winds prior to the nominal spring transition of prevailing winds. Transition to the southward summer form is usually not complete until the prevailing summer northerlies are well-established, although the 1985 images show that this transition can be completed in a matter of days.

3.4. *Summer reversal*

A response of the plume to high-frequency wind variability is illustrated by two CZCS images from 1979 (figure 5). On May 19, the plume is in a well developed summer form, long and oriented SWS, following spring transition on 8 May. Prevailing summer northerlies were interrupted by a southerly wind event on 7–11 July. On 14 July, the plume is short and oriented W of the river mouth, with some plume water flowing north. Other imagery (e.g. 9 and 18 June 1985, see the table) shows that the plume returns to the summer form when winds return to normal after such a summer reversal.

Three other summer plume reversals were seen in the satellite imagery (6 July 1980, 12 May 1983 and 9 June 1985), shortly after very weak and brief southerly wind events. These observations suggest that the plume moves to the north, with the Coriolis deflection, much more readily than to the south.

3.5. *Coastal upwelling*

The pair of images in figure 6 illustrate that upwelled water replaces Columbia River plume water as the most important component of Washington–Oregon coastal waters in late summer. In 1983, summer northerly winds prevailed from 4 April to 14 October, although southerly winds occurred during 9–11 and 20–23 September.

In an AVHRR image from 21 September, coastal upwelling is indicated by cold water along the coast. Note the long streamers of very cold water extending offshore from the Oregon coast south of the Columbia River mouth. Coastal upwelling increases to the south of the river mouth, reaching a regional maximum at 40°N (Bakun 1975). Plume water can be discerned at the river mouth as a very small patch of warm water that seems to be turning north in response to the anomalous southerly winds. The structure of the green water in the CZCS image from 20 September is dominated by phytoplankton produced in the cold, nutrient-rich upwelled water.

From July until September, as upwelling strengthens and river flow declines, the

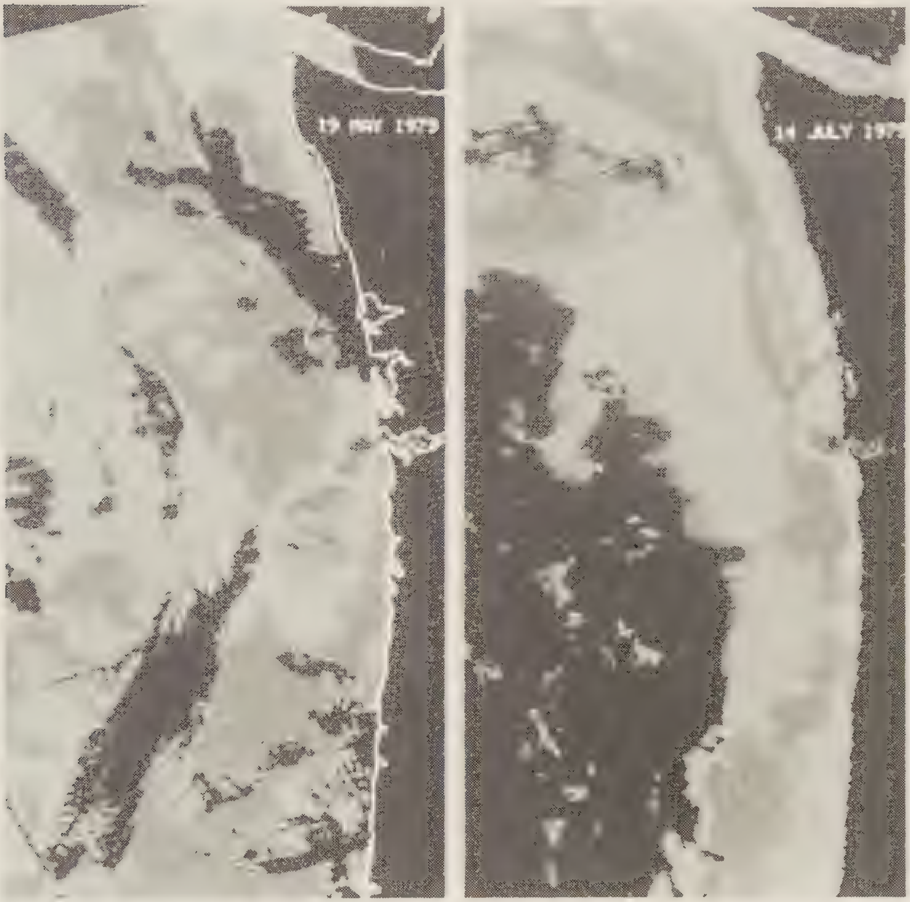

Figure 5. CZCS images illustrating the response of the Columbia River plume to a reversal of the summer prevailing winds during 7–11 July 1979.

plume can only barely be discerned in temperature images and cannot be differentiated from upwelled water in colour images. In our experience, this is the only time of year when the plume is more readily discernible in temperature imagery than in colour imagery.

3.6. *Tidal pulsing*

A CZCS image from 24 May 1982 (figure 7) shows the segmental structure of the plume, which is often evident in early summer when river flow is at its maximum. This pattern may be attributed to tidal pulsing of the river flow. Tidal currents reverse the flow at the mouth, causing two pulses of up to 10^9 m^3 of river water to enter the ocean daily. Each pulse is equivalent to a patch 2 m deep and up to 20 km in diameter, consistent with measured salinity distributions in the plume (Barnes *et al.* 1972) and with the pattern seen in this image. Identification and tracking of individual pulses could aid studies of mixing and productivity in these waters.

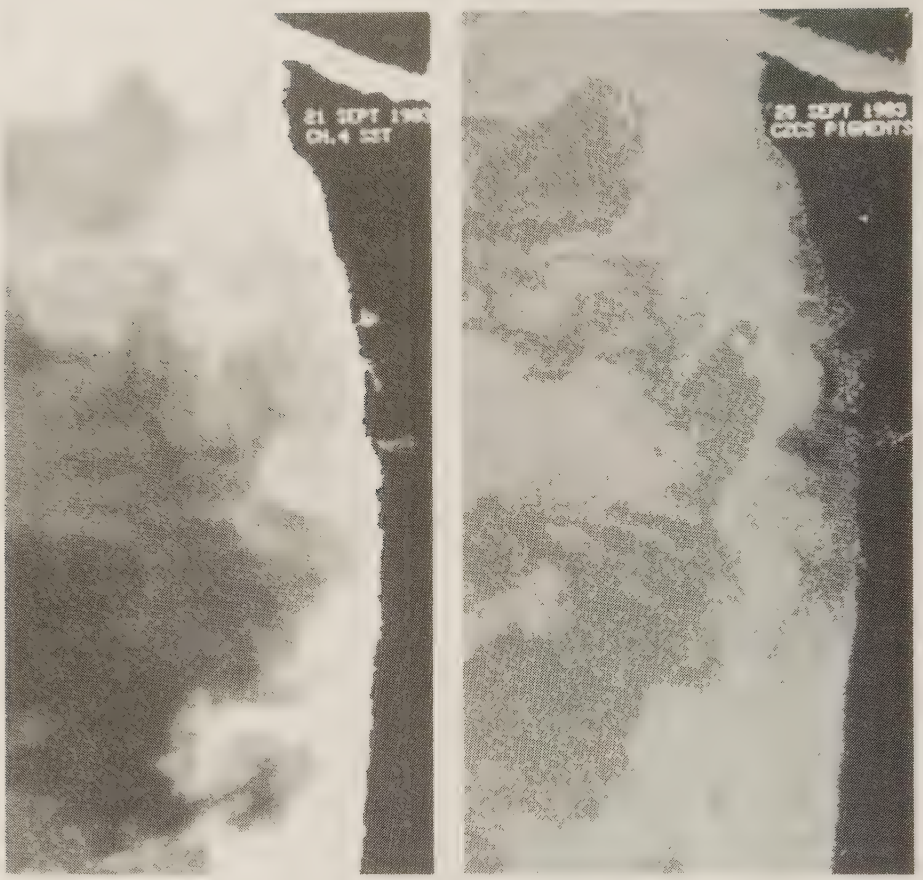

Figure 6. A pair of AVHRR and CZCS images, from 21 September 1983, illustrating the Columbia River plume region during strong summer upwelling. In the AVHRR image, cold sea surface temperatures are light grey and warm temperatures are dark grey.

4. Conclusions

The Columbia River plume has long been recognized as an important component of the coastal Pacific Ocean between Vancouver and northern California. However, it has been difficult to study and monitor its variability by shipboard sampling alone. Visible and infrared sensors on satellites offer the frequent and synoptic coverage of this region needed to follow the plume's rapid responses to seasonal and higher frequency forcing. We found that the plume was almost always more clearly defined in CZCS colour imagery than in AVHRR sea surface temperature imagery, because the magnitude and sign of the temperature difference between plume water and coastal ocean water varied seasonally. Remote sensing studies of such river plumes could be enhanced in the future by quantifying the visible–infrared signature of the plume. For example, the colour of plume water is determined by sediments and other substances, as well as by phytoplankton pigments, so a more appropriate pigment algorithm could perhaps differentiate plume and upwelled waters in CZCS imagery.

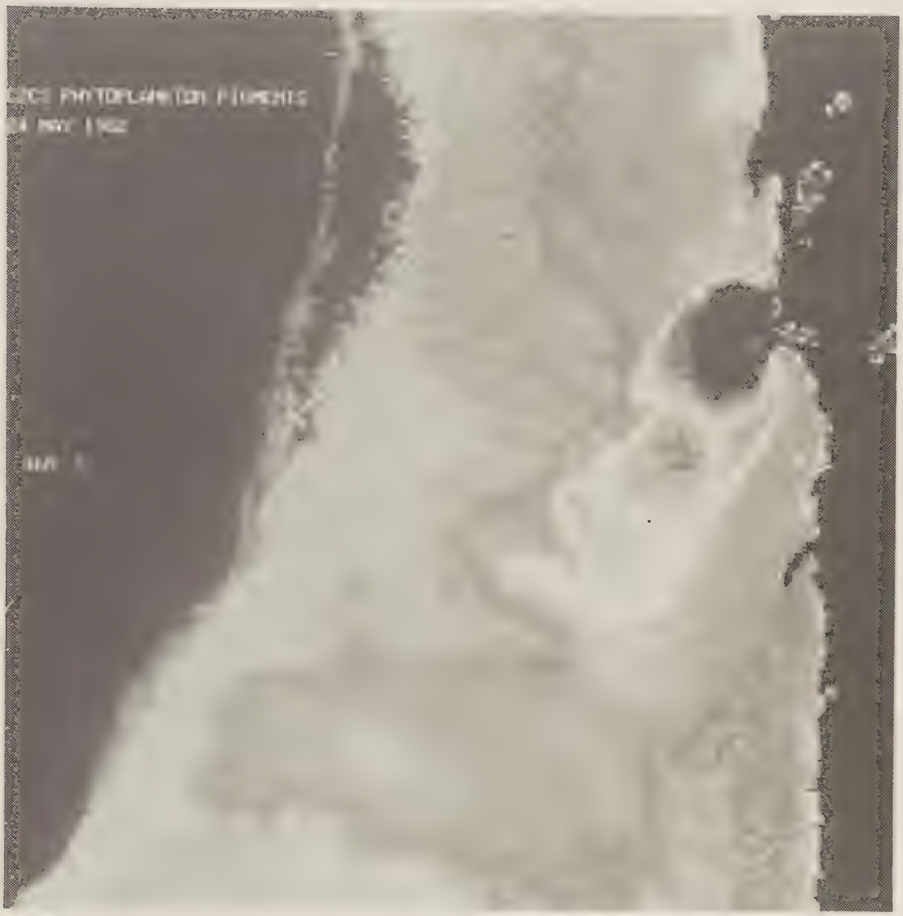

Figure 7. CZCS image, from 24 May 1982, illustrating the Columbia River plume during peak river flow in early summer.

Acknowledgments

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References

BAKUN, A., 1975, Daily and weekly upwelling indices, west coast of North America, 1967–1973. NOAA Technical Report NMFS SSRF-693.

BARNES, C. A., DUXBURY, A. C., and MORSE, B., 1972, Circulation and selected properties of the Columbia River effluent at sea. In *The Columbia River Estuary and Adjacent Ocean Waters: Bioenvironmental Studies*, edited by A. T. Pruter and D. L. Alverson (Seattle: University of Washington Press), pp. 71–80.

GORDON, H. R., BROWN, J. W., and EVANS, R. H., 1988, Exact Rayleigh scattering calculations for use with the Nimbus-7 Coastal Zone Color Scanner. *Applied Optics*, **27**, 862–871.

GORDON, H. R., CLARK, D. K., BROWN, J. W., BROWN, O. B., EVANS, R. H., and BROENKOW, W. W., 1983, Phytoplankton pigment concentrations in the Middle Atlantic Bight: comparison of ship determinations and CZCS estimates. *Applied Optics,* **22,** 20–36.

GORDON, H. R., and MOREL, A. Y., 1983, *Remote Assessment of Ocean Color for Interpretation of Satellite Visible Imagery* (New York: Springer-Verlag).

GOWER, J. F. R., 1985, Reduction of the effect of clouds on satellite thermal imagery. *International Journal of Remote Sensing,* **6,** 1419–1434.

HICKEY, B. M., 1979 a, The California Current system—hypotheses and facts. *Progress in Oceanography,* **8,** 191–279.

HICKEY, B. M., 1979 b, Hydrographic observations over the Washington–Oregon continental shelf during WISP (February–March 1975). University of Washington, Department of Oceanography, Special Report No. 65.

HUYER, A., 1979, Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. *Limnology and Oceanography,* **22,** 442–453.

HUYER, A., PILLSBURY, R. D., and SMITH, R. L., 1975, Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. *Limnology and Oceanography,* **29,** 90–95.

LAURITSON, L., NELSON, G. J., and PORTO, F. W., 1979, Data Extraction and Calibration of TIROS-N/NOAA Radiometers. NOAA Technical Memorandum NESS 107.

MCCLIMANS, T. A., 1979, On the energetics of river plume entrainment. *Geophysical and Astrophysical Fluid Dynamics,* **13,** 67–81.

NEAL, V. T., 1972, Physical aspects of the Columbia River and its Estuary. In *The Columbia River Estuary and Adjacent Ocean Waters: Bioenvironmental Studies*, edited by A. T. Pruter and D. L. Alverson (Seattle: University of Washington Press), pp. 19–70.

STRUB, P. T., ALLEN, J. S., HUYER, A., and SMITH, R. L., 1987 a, Large-scale structure of the spring transition in the coastal ocean off western North America. *Journal of Geophysical Research,* **92,** 1527–1544.

STRUB, P. T., ALLEN, J. S., HUYER, A., SMITH, R. L., and BEARDSLEY, R. C., 1987 b, Seasonal cycles of currents, temperatures, winds, and sea level over the northeast Pacific continental shelf: 35° N to 48° N. *Journal of Geophysical Research,* **92,** 1507–1526.

ZHANG, Q. H., JANOWITZ, G. H., and PIETRAFESA, L. J., 1987, The interaction of estuarine and shelf waters: a model and applications. *Journal of Physical Oceanography,* **17,** 455–469.

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QUANTITATIVE DETERMINATION OF OPTIMUM SUSTAINABLE POPULATION LEVEL

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ABSTRACT

Quantitative methods are reviewed and compared for determining whether a marine mammal population is at an optimum sustainable population (OSP) level, a management goal specified by the U.S. Marine Mammal Protection Act. Methods of OSP determination fall into two general types: those that require an estimate of a population's maximum net productivity level (*e.g.,* the back-calculation method) and those that do not (*e.g.,* dynamic response analysis). The two types differ in the data they require and in whether they determine OSP with respect to present or historical carrying capacity. Back-calculation and dynamic response analyses are compared using data on the California gray whale (*Eschrichtius robustus*). Marine mammal monitoring programs should be designed to detect trends in both the abundance of a population and its condition relative to carrying capacity, because both quantities are involved in the definition of OSP. The value of using both abundance and condition indices in an assessment is illustrated with data on the northern fur seal (*Callorhinus ursinus*).

Key words: back calculation, dynamic response analysis, management, Marine Mammal Protection Act, optimum sustainable population.

The U.S. Marine Mammal Protection Act (MMPA) of 1972 specified that each marine mammal population should be maintained at an "optimum sustainable population" (OSP) level. This phrase was somewhat vague because it lacked an operational definition in existing management terms. Nevertheless, the MMPA represented a fundamental change in marine mammal management by recognizing that all organisms live in necessary interdependence with each other, and that the value of a marine resource should not be measured by economic criteria alone.

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Unfortunately, the new management perspective has been difficult to implement, not only because of insufficient knowledge of the biology and ecology of marine mammal species, but also an insufficient theoretical foundation. Biological resource management with an ecosystem perspective is a relatively new concept, whereas management based on the dynamics of single species has a longer history of development and application in fisheries and wildlife biology. In practice, management of marine mammals has relied on concepts of single-species population dynamics. The U.S. National Marine Fisheries Service has defined OSP as a population level between carrying capacity and the population size at maximum net productivity (Federal Register, 21 December 1976, 41FR55536). A key point is that the maximum net productivity level (MNPL) forms the lower boundary of OSP range. In practice, therefore, the problem of establishing whether a marine mammal population is "optimum" usually involves determining whether it is above its MNPL.

Qualitative measures of OSP status have been proposed and used on a preliminary basis in the past, but more rigorous and quantitative methods are needed. There is not at present, nor is there likely to be in the future, any single analysis that is best in all situations. The selection of an analysis always depends on the available data, which, in turn, depend on the biology of the species being managed. In addition, because marine mammals "combine the problems of inaccessibility common to fish populations with the variability in behavior characteristic of terrestrial mammalian species" (Eberhardt *et al.* 1979, p. 6), consideration of new ways of determining OSP status is severely constrained by the types of data we are able to collect.

This paper reviews and compares quantitative methods presently available for determining, within the present definition of OSP, whether a population is in OSP range. Because OSP determinations may be challenged by various interest groups, the determination procedures should be scientifically credible and legally defensible (Bean 1983). Our specific evaluations apply to marine mammals under U.S. jurisdiction only, but the discussion of general approaches being attempted has wider applicability as many countries implement new principles of management of living resources (Holt and Talbot 1978).

Review of Current Procedures

For many marine mammal populations, few harvest data are available, and traditional fisheries methods of estimating MNPL from catch records are of little help. This has led to some new approaches to determine whether a marine mammal population is in OSP range. For heuristic purposes, approaches to OSP determination may be divided into two types: those that require an estimate of MNPL and those that do not.

Methods Requiring an Estimate of MNPL

A direct approach to determining OSP status is to estimate MNPL for the marine mammal population in question and compare this number to the current estimated population size. This approach depends on the data available to estimate present population size, carrying capacity, and MNPL as a fraction of carrying capacity.

Present population size—The present population size must be measured in the same units in which carrying capacity is measured. For marine mammals, this unit will usually be absolute numbers of animals but could be some relative measure correlated with population size.

Carrying capacity (maximum sustainable population)—As normally used in applied population dynamics, carrying capacity refers to an equilibrium population level under conditions of no harvest. Human activities which lead to habitat degradation or loss may reduce the carrying capacity. The intent of the MMPA, however, clearly was not to condone alteration of marine mammal habitat; a reduction in carrying capacity due to habitat degradation may lead to a marine mammal stock being classified as depleted. Consequently, in the context of OSP determination and as used in this paper, carrying capacity refers to an equilibrium population level before impact by man, either direct (through harvest or incidental killing) or indirect (through habitat degradation or harvest of predator, prey, or competitor species). Unfortunately, carrying capacity in this sense can be difficult to measure, because few marine mammal populations today have not been impacted by man in some way. Furthermore, the species of greatest concern are those that have declined through the influence of man.

The primary technique for estimating carrying capacity has been the back-calculation method. Important assumptions of this approach are that the historical population, before substantial impact by man, was at equilibrium and that the environment has not changed greatly. Under these conditions, a past population size may be taken as an estimate of current carrying capacity. Back calculation relies on a knowledge of the population dynamics of the species and has affinities with what is known as "cohort analysis" in the fisheries literature (Ricker 1975). Birth and natural mortality rates or their difference, the net recruitment rate, are used to project the population backwards in time. Known losses in the form of harvests or incidental kills are used at each time step to calculate previous population size. The back-calculation method was used to estimate carrying capacity for several dolphin (*Stenella* spp.) populations during the status-of-porpoise-stocks determinations of 1976 and 1979 (Smith 1983). Ohsumi (1976), Reilly (1981), Cooke (1986), and Lankester and Beddington (1986) conducted back-calculation analyses for gray whales (*Eschrichtius robustus*). Breiwick *et al.* (1981, 1984) used variations of this method, including a time lag to allow for the period between birth and vulnerability to harvest, to estimate the 1848 abundance of bowhead whales (*Balaena mysticetus*) in the North Pacific prior to commercial whaling.

Smith and Polacheck (1979) investigated the sensitivity of the back-calculation method. In general, the reliability of estimates of historical population size depends on the reliability of the estimates of all of the quantities required—vital rates, numbers killed by man, and present population size. Which of these quantities is most important to the accuracy of the carrying capacity estimate depends on how far back into the past we project the population and on the relative importance of man-induced to natural mortality. The method would work well, for example, with a population that had suffered a relatively recent decline dominated by known losses. The method is less useful if incidental kills are not known (and thought to be substantial) or if the time of the pre-exploitation population level is so far in the past that the estimate of carrying capacity is heavily dependent on the values chosen for the (usually poorly known) vital rates.

The back-calculation method also requires the specification of a density-dependent function for the vital rates. The usual choice has been a generalized logistic formulation (Allen 1976, Gilpin *et al.* 1976). The calculations of Smith (1983) showed that estimates of carrying capacity could be quite sensitive, particularly at realistic maximum rates of increase, to the choice of the exponent in the generalized logistic function. Lankester and Beddington (1986) and Cooke (1986) questioned the internal consistency of the density-dependent function traditionally used by the International Whaling Commission with known population trends and catch history of the gray whale.

A second approach to estimating capacity would rely on the measurement of some limiting resource for the population, such as food supply or haul-out sites. The validity of such estimates depends on sufficient knowledge of the species' ecology to demonstrate that the resource in question will, in fact, be limiting. Demonstrating this limitation from first principles is a daunting challenge. Consider food. An estimate of carrying capacity based on food supply would depend, at a minimum, on a knowledge of prey abundance, dietary preferences, metabolic requirements, and energetic conversion efficiencies. Most are dynamic quantities that change with population level, age, location, and physiological condition, not static quantities that need only be measured once. Knowledge of dietary preferences, for example, should include the population dynamics of prey populations and alternate prey sources as preferred prey become scarce. Thus, estimating carrying capacity by a limiting resource may imply, in theory, a rather complete understanding of the whole ecosystem in which the marine mammal lives.

A simplified and more practical variant of this approach is to demonstrate that an unharvested population is at equilibrium within a portion of the range. If density is known for that area, carrying capacity may be estimated as the product of the density of animals at equilibrium and the total area of available habitat. Such calculations have been used for sea otters (*Enhydra lutris*) in Alaska and California (Kenyon 1969, Estes and Palmisano 1974), but problems of scale and measurement of available habitat may arise (J. A. Estes, in preparation. Growth patterns in sea otter populations. Institute of Marine Sciences, University of California, Santa Cruz, CA 95064).

MNPL as a fraction of carrying capacity—In the absence of harvest data and observation of the population's dynamics over a wide range of population sizes, this parameter is difficult to estimate for a particular species. For most marine mammals, we rely on theoretical models of population dynamics and on general patterns revealed by comparative studies to provide estimates of MNPL as a fraction of carrying capacity. According to the widely used logistic model, MNPL is at half the carrying capacity. Eberhardt and Siniff (1977) suggested that the demography of marine mammals leads to an MNPL at more than half the carrying capacity and, hence, that the lower limit of OSP range might lie closer to carrying capacity than specified by the logistic model. Fowler (1981) expanded on this theme, using theoretical arguments and empirical evidence to draw a contrast between some organisms with short lives, high reproductive rates, and production curve peaks shifted to relatively low population levels (*e.g.*, most fish) and other organisms with long lives, low reproductive rates, and production curve peaks shifted to relatively high population levels (*e.g.*, marine mammals). Fowler (1984, 1988) further demonstrated, for a wide variety of organisms, a high correlation between MNPL as a fraction of carrying capacity and the logarithm of the rate of increase per generation. This correlation is an important development because it could allow us to predict the position of MNPL as a fraction of carrying capacity on the basis of population parameters that are independent of harvest information and do not require observing the population at a wide range of sizes. However, the intrinsic rate of increase and generation time of the species must still be estimated.

During the status-of-porpoise-stocks determinations of 1976, MNPL was considered to be in the range of 0.5–0.7 as a fraction of carrying capacity, whereas in 1979, a range of 0.65–0.80 was used (Smith 1983). Although these numbers were based on the best available data, the range for MNPL, combined with uncertainty in other parameters, allowed room for several possible interpretations and did not clearly settle whether some dolphin stocks had been depleted below OSP. This led to a search for alternative methods.

Methods Not Requiring an Estimate of MNPL

Goodman (1988) recognized that the minimum information required to make an OSP determination is simply whether the present population is above or below MNPL, and that this need not require actual estimates of MNPL or even the present population size. Although there may be some cases in which a population is temporarily above carrying capacity and not in OSP range, the more typical problem is trying to determine on which side of MNPL the population currently lies. The essence of this approach is to find a parameter related to population size that can indicate whether the population is above or below MNPL, without having to estimate that level itself. Let us call such a parameter an OSP measure.

Eberhardt and Siniff (1977) proposed 12 criteria for establishing a relative population level:

Behavioral attributes
    1) Antagonistic and/or displacement behavior
    2) Time spent in searching for food or in tending and feeding young
    3) Shifts in dietary components
Individual responses
    4) Physical condition, including growth rates
    5) Incidence of disease and parasitism

Reproductive characteristics
  6) Age at first reproduction
  7) Annual reproductive rates of mature females
Populational aspects
  8) Age structure
  9) Survival rates, especially of young
  10) Occupancy of marginal range
  11) Rate of change of population size
  12) Effects on habitat or food base

The way in which these criteria change with population size is usually apparent. For example, as a population nears carrying capacity, age at first reproduction should increase and individual growth rates should decrease. The magnitude and relative importance of the changes are far from obvious, however. As noted by Eberhardt and Siniff (1977), we do not know how to scale these criteria to population size. Their usefulness, therefore, is to indicate in a general way whether a population is near carrying capacity or far from it. This qualitative approach has been used previously by the National Marine Fisheries Service to assess many species of marine mammals when data on historical take were not available. Can any of the above criteria be sufficiently quantified to be used as an OSP measure?

Let us consider the desirable characteristics of an OSP measure. First, the OSP measure should be an easily measurable aspect of the population. Among the 12 criteria listed above, some are much easier to measure than others. Incidence of parasitism might be a good indicator of population status, but difficulties in measuring this parameter might preclude its use for many populations. A distinction also should be drawn among the above criteria according to whether they are individual or population measures. The first five criteria are measurable for an individual animal; provided variation for the character among individuals is not excessive, a sample of a few animals might suffice. The last seven criteria are population characteristics not defined for an individual. They require collection of an unbiased sample of a number of individuals, a more difficult type of datum to collect. Then again, certain criteria, such as dietary composition, disease, and occupancy of marginal range, might only require determining presence or absence. If such measures could be defined quantitatively in terms of an OSP level, they would have considerable appeal because of the relative ease of data collection.

A second desirable characteristic of an OSP measure is a highly consistent relationship to population size. Variance in the OSP measure should be small, allowing it to be used as a surrogate for population size. If there is no harvest or incidental take, the relationship of the measure to actual population size need not be known, because a relative scale is sufficient (Goodman 1988). The measure should also be uninfluenced by other conditions. If shifts in diet composition are used to indicate changes in population size, for example, they should depend on population size of the marine mammal only and not on changes in the relative abundance of different prey species.

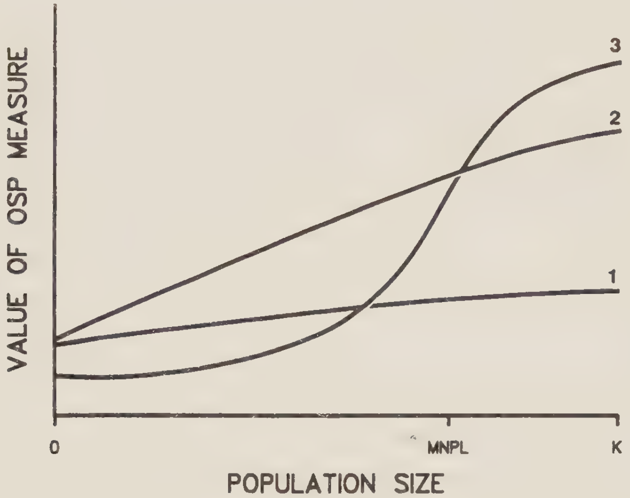

Figure 1. Hypothetical curves of three OSP measures as a function of population size.

Third, a practical OSP measure undergoes an easily detectable change as a function of population size. Even if easy to measure and tightly correlated with population size, an OSP measure will not be useful if the degree to which it changes with population size is small with respect to our ability to measure it (curve 1 in Fig. 1). Adult survival rates might be sensitive to population size, but the difference in survival rates between a population below its MNPL and one above its MNPL is probably too small for us to measure reliably. A more useful OSP measure would have a large range of values (curve 2 in Fig. 1), and its rate of change would be greatest in the vicinity of MNPL (curve 3 in Fig. 1).

Fourth and perhaps most critically, the value of the OSP measure above and below MNPL must be known so that the value can be related to an OSP level. This is a difficult requirement. For example, to be an OSP measure, the age at first reproduction that would indicate whether the species is above or below its MNPL must be specifiable. Although the trend of the indicator might be predictable (*e.g.*, an increasing age at first reproduction will accompany increasing population size), predicting a specific critical value *a priori* is beyond our present knowledge. It might be possible to discover empirically what ages at first reproduction indicate a population is below MNPL *if* there were some independent way, at the same time, of assessing population status relative to MNPL. But if there were this other independent measure, age at first reproduction would not have to be used. Thus, a critical value of an OSP measure as a function of population size will have to be predicted on theoretical grounds. Furthermore, to withstand legal scrutiny and challenge, the OSP measure must be based on a widely accepted model of population dynamics.

The technique available at present that most closely satisfies these four characteristics is dynamic response analysis (Goodman 1988). Because the analysis depends only on the mild assumption of a unimodal production curve, it is based on a widely accepted feature of population dynamics. Moreover, its metric—acceleration or deceleration of population growth—undergoes a known change precisely at MNPL. From a theoretical viewpoint, this new method appears quite useful. The practical requirements for satisfactory performance with a non-harvested species are a sufficiently long and precise sequence of a population abundance index (Gerrodette 1988). Dynamic response analysis has been used with the California sea lion (*Zalophus californianus*) (DeMaster *et al.* 1982) and northern elephant seal (*Mirounga angustirostris*) (Boveng *et al.* 1988).

Comparison of Two Methods to Assess OSP Status

Reilly (1981) performed numerous back calculations for gray whales. The simulation using historical (*ca.* 1800) carrying capacity of 24,000 whales resulted in a population trajectory that agreed most closely with the known history and exploitation of the species. In 1980, an estimated 15,647 gray whales comprised the North American population (Reilly *et al.* 1983). Thus, according to this analysis, gray whales in 1980 were about 65% of their historical maximum sustainable level, a figure placing them presumably at the lower end of OSP range.

We carried out a dynamic response analysis (see Boveng *et al.* (1988) for a description of methods) on gray whales for the period 1967–80, using the 13 yr of population estimates in Reilly *et al.* (1983). The pattern formed by plotting the second-order coefficients for a series of polynomial regressions against time (Fig. 2) is indicative of a population that initially (1967) was below MNPL and at the end (1980) was above MNPL. Most of the second-order coefficients were not significantly different from 0, but the pattern using 6–11 census periods was consistent: Coefficients were positive, declined to a minimum less than 0, then increased but usually remained negative (Fig. 2). Therefore, according to this analysis also, the California gray whale population was in OSP range in 1980.

This comparison provides compelling reasons for researchers to design their monitoring programs to collect, if possible, data needed to perform both methods of OSP determination. An assessment based on two relatively independent methods is much stronger. Moreover, because different kinds of data are used, agreement or disagreement between the two methods may give additional insights. For example, the agreement between the two methods strengthens Reilly's (1981) conclusion that California gray whales were in OSP range. It also suggests that, because back calculation assesses the population relative to historical carrying capacity while dynamic response analysis assesses it relative to current carrying capacity, the maximum sustainable population of gray whales has not changed greatly in the last 180 yr.

Abundance Indices and Condition Indices

The definition of OSP involves the relation between two quantities: population size and carrying capacity. Both quantities may change. DeMaster (1984) pointed

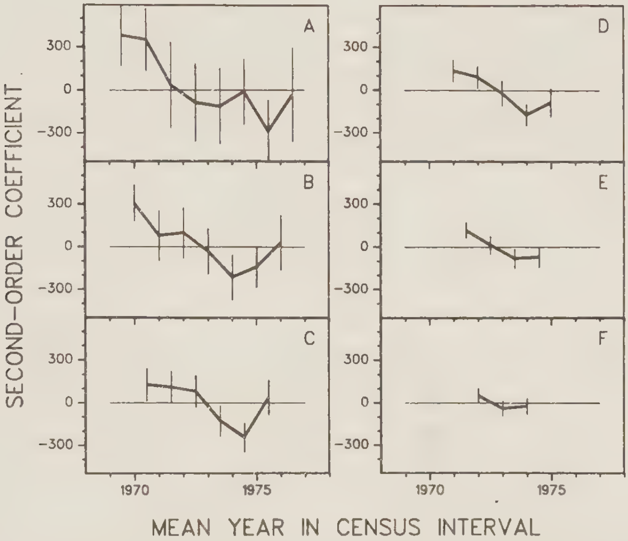

Figure 2. Dynamic response analysis for the California gray whale, 1967-80, using the method of Boveng *et al.* (1988). The second-order regression coefficient is plotted against the mean year in the sequence of censuses. Vertical bars are ±1 standard error. The different panels plot coefficients against sequences of censuses of different lengths. (A) 6 yr, (B) 7 yr, (C) 8 yr, (D) 9 yr, (E) 10 yr, and (F) 11 yr.

out that previous monitoring programs have confused abundance indices with condition indices. An abundance index measures an aspect of a population related to actual numbers of animals. Examples of abundance indices are number of pups or calves, number of territorial males, and number of sightings per kilometer. A condition index, on the other hand, measures the condition of a population relative to its resources. The 12 criteria of Eberhardt and Siniff (1977) listed above are condition indices.

A change in population size does not necessarily mean a change in OSP status, because carrying capacity might also have changed due to natural causes. Monitoring programs should therefore be designed to measure both abundance and condition indices. By knowing the trends in both types of indices, changes in carrying capacity may be deduced (Table 1). For example, if a condition index worsens, the population is nearer its carrying capacity, but if, at the same time, an abundance index has not changed, we may conclude that the carrying capacity of the environment for that species has declined (top center cell in Table 1). This is, no doubt, a simplistic way of viewing the complicated relations between a population and its environment, but it is surely less simplistic than assuming a constant environment.

The utility of monitoring both abundance and condition indices may be illustrated with the northern fur seal (*Callorhinus ursinus*). Of the numerous indices available for the Pribilof Islands population, we chose two as examples: number of pups born (an abundance index) and pup mortality rate on the rookery (a condition index). Both have declined over the last 16 yr (Fig. 3).

Table 1. A decision matrix for determining changes in carrying capacity (*K*) indicated by changes in an abundance index and a condition index.

Condition index	Abundance index		
	Decrease	No change	Increase
Worse	*K* much lower	*K* lower	No change in *K*
No change	*K* lower	No change in *K*	*K* higher
Better	No change in *K*	*K* higher	*K* much higher

The decline in the abundance index could be ascribed to a reduction in carrying capacity; however, the declining pup mortality rate indicates that the population has been decreasing relative to its carrying capacity. The combination of changes in these two indices, therefore, is consistent with a population declining relative to a constant carrying capacity during this period (lower left cell in Table 1). The lack of change in carrying capacity is supported when the two indices are compared over a longer period. Pup mortality rate, as a function of number of pups born, has evidently been the same during recent years as it was early in the century when the population was at or below its present level (Fig. 4). Had carrying capacity declined, one would expect that the points for the last 16 yr (solid dots) would fall above points for earlier years, but this has not been the case.

Discussion and Conclusion

The current operational definition of OSP utilizes the concept, derived from fisheries management, of an MNPL. Confusion has sometimes arisen between MNPL and maximum sustainable yield (MSY) levels. Some authors have tried to use the MSY level as the lower boundary of OSP range (Bean 1983). This is unfortunate because the MSY level for a population is a function of its age structure as well as the age and sex composition of the harvest. The MSY level is undefined except in relation to a particular harvest; a population has no single MSY level. For example, if only pups are harvested, the MSY level for the Weddell seal (*Leptonychotes weddelli*) is 0.55 of carrying capacity, whereas if only adults are harvested, the MSY level is 0.69 (DeMaster 1981). By contrast, the MNPL is defined in the absence of a harvest as a function of the way birth and death rates change with density. The MNPL is usually taken to be that single level that would occur with no harvest, but if a harvest or other perturbation has displaced the population from a stable age and sex structure, there may be a different transient MNPL as the population recovers.

The need to regulate the take of marine mammals, particularly the incidental catch of *Stenella* spp. in the purse-seine tuna fishery, has stimulated the development of quantitative methods of OSP determination. Two general approaches have been attempted. One, exemplified by the back calculation of pre-exploitation dolphin population size in the eastern tropical Pacific (Smith 1983), requires the estimation of carrying capacity and MNPL. The other, represented

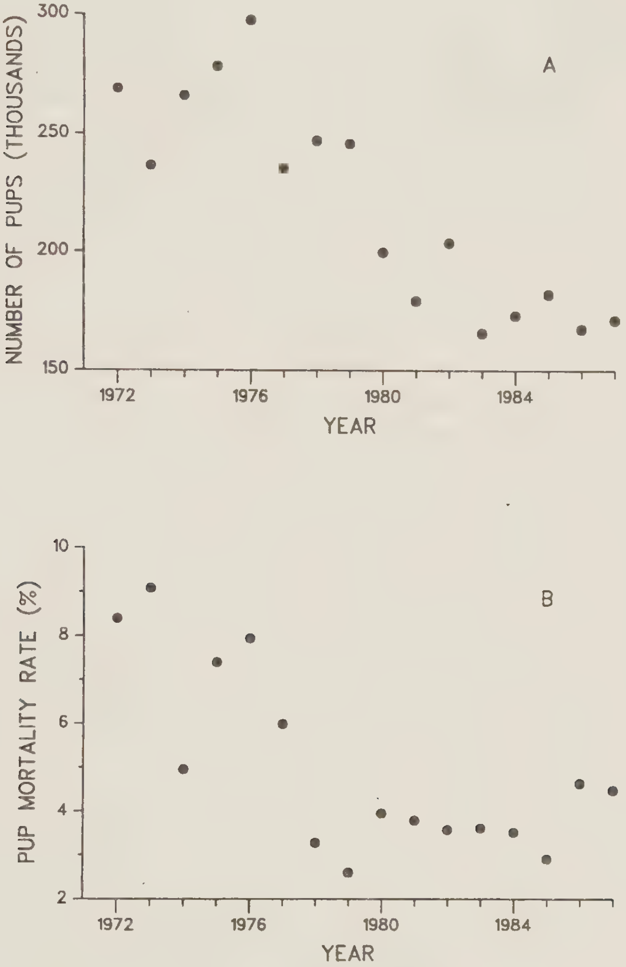

Figure 3. Trends in (A) births and (B) pup mortality rates for northern fur seals on St. Paul Island, Alaska, 1972–87. Data are from Lander (1980), York (1985), and, for recent years, unpublished records at the National Marine Mammal Laboratory, Seattle.

by dynamic response analysis (Goodman 1988), avoids the need to estimate carrying capacity and MNPL by considering the recent history of a population's dynamics. Which approach is more useful depends on the data available.

A dynamic response analysis requires a temporal sequence of an abundance index, augmented by data on mortality due to harvest or incidental kill. Because an estimate of population size (or at least an index of population size) is part of many monitoring programs, this type of datum may commonly be available. Whether such data are of sufficient number and precision for dynamic response analysis to be useful is a major question. For the precision of population estimates likely to be achieved with most marine mammals, and given reasonable pop-

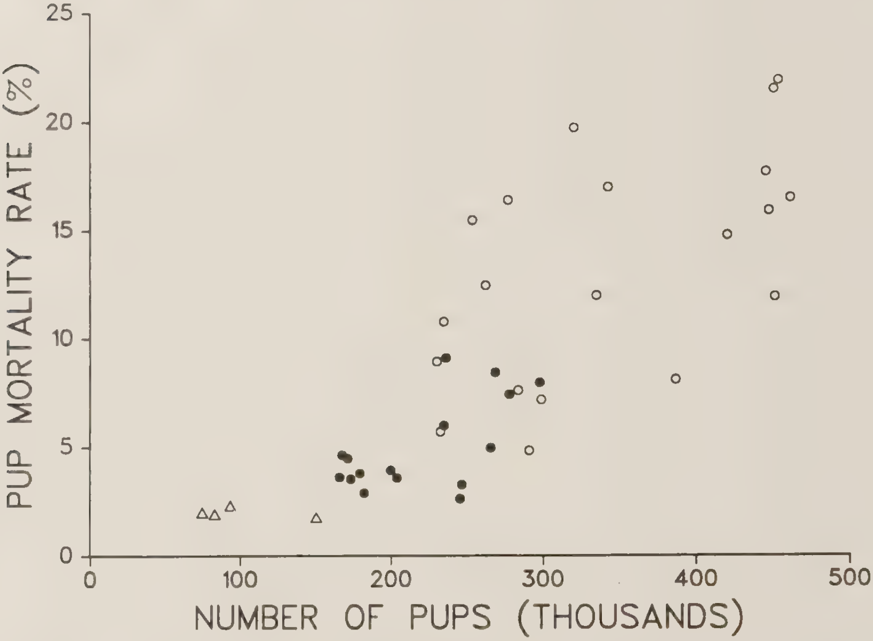

Figure 4. Mortality rate of northern fur seal pups as a function of number of pups born on St. Paul Island, Alaska, for various years within three time periods: 1914–22 (△), 1950–70 (○), and 1972–87 (●). Data are from Lander (1980), York (1985), and, for recent years, unpublished records at the National Marine Mammal Laboratory, Seattle.

ulation growth rates, it appears that a minimum of about 10 annual population indices are required (Boveng *et al.* 1988, Gerrodette 1988). Further study of the statistical power of dynamic response analysis with both simulated and actual data is needed, particularly, as with the California gray whale, when the population growth rate is low and curvature is barely detectable.

On the other hand, a back-calculation analysis does not require a time series of population size estimates. It does require an estimate of current population size, estimates of past birth and death rates of the population, again augmented by data on incidental kills or harvest, and knowledge of where MNPL falls as a fraction of carrying capacity. Data requirements are greater than for dynamic response, and the data are not used as efficiently to answer the specific management question at hand (Goodman 1988). Partly because of difficulties in applying this technique to determine OSP for eastern tropical Pacific dolphin populations, the MMPA was amended in 1984 to authorize the taking of certain dolphin populations without having to make an OSP determination (Marine Mammal Commission 1986).

Different methods of OSP determination may also be contrasted by the meaning attached to carrying capacity. Whether current or historical carrying capacity is to be used when making an OSP determination is presently an unresolved issue in marine mammal management. To allow carrying capacity (as used in an OSP determination) to be reduced when habitat is lost is contrary to the spirit of the MMPA, but the acceptance of historical carrying capacity as the standard in all cases is also unreasonable. When reversible changes have taken place in the habitat, efforts should be made to restore the "health and stability" of the ecosystem. But some changes have been made that, for all practical purposes, are irreversible. In such cases, we must have some way of making an OSP determination in relation to current carrying capacity, even though the population has never been observed at that level.

Back calculation is, by definition, an attempt to estimate historical carrying capacity. However, carrying capacity could also be measured in current terms, by available food for example. A complicating factor in this case is that prey abundance may change with time, and if prey species also are harvested, the amount of fishing may have a substantial impact on the estimated carrying capacity. Dynamic response analysis measures OSP status in current terms when used with the most recent sequence of population estimates, but it could also be used to measure historical carrying capacity when used with a sequence of past population estimates. The analysis gives an estimate of OSP status pertaining to the time spanned by the sequence of population estimates.

Relative OSP measures that do not require a population's MNPL to be estimated have several advantages over those that do. However, such OSP measures must have certain practical and theoretical characteristics. They must be easily measured, highly consistent, sufficiently detectable and have a theoretically derivable critical value indicating whether a population with such a value is above or below its MNPL. Because of the need to derive a critical value theoretically, the outlook for developing a quantitative OSP measure from the criteria of Eberhardt and Siniff (1977) or the general regulatory model of Eberhardt (1977) is doubtful. Dynamic response analysis may succeed because what it uses as a critical value, a change from accelerating to decelerating population growth, is the *definition* of MNPL. To rest on as solid a theoretical foundation, any other OSP measure developed in the future will similarly have to use as its metric a quantity that is part of the definition of MNPL.

Marine mammal monitoring programs usually try to estimate the size of some accessible portion of the population. While such information can at least indicate trends in population size, and dynamic response analysis was developed in response to such data-poor situations, we need other kinds of information to improve management of marine mammal populations. For one thing, the inevitable errors associated with estimating an abundance index mean that data must be collected over a number of years before a trend is statistically significant. Although the number of years required to detect a trend can be estimated (Gerrodette 1987), the trend can be detected only after it has happened. For long-lived, slowly reproducing animals such as marine mammals, this is usually too late for effective management. The result may be a succession of "crisis" responses. Fay *et al.* (1989) showed how inadequate monitoring and poor communication have caused the Pacific walrus (*Odobenus rosmarus*) to fluctuate through three wide cycles in population size over the last 150 yr. Monitoring a population condition index in addition to an abundance index has the potential to detect demographic changes at an earlier stage and also provides a complementary type of information useful in management (Table 1).

If our assessment of the current situation is correct, it would be worthwhile to develop more approaches to making quantitative OSP determinations. As noted earlier, any consideration of new approaches must keep in mind the type of data that can be collected for marine mammal populations. One possible new approach is to explore ways of combining several qualitative but independent measures of population status. It is also important to remember that all of this discussion has taken place within the framework of the current single-species definition of OSP. A more long-term solution is to develop the theoretical and practical tools for true ecosystem management. Assessment of the data necessary to make informed management decisions in the controversial area of the impact of seals on fisheries is a first step toward this goal (Beddington *et al.* 1985, Gulland 1987, Harwood and Croxall 1988).

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Literature Cited

Allen, K. R. 1976. A more flexible model for baleen whale populations. Reports of the International Whaling Commission 26:247–263.

Bean, M. J. 1983. The evolution of national wildlife law. Praeger Scientific, Urbana, IL. 448 pp.

Beddington, J. R., R. J. H. Beverton and D. M. Lavigne, eds. 1985. Marine mammals and fisheries. George Allen & Unwin, London. 354 pp.

Boveng, P., D. P. DeMaster and B. S. Stewart. 1988. Dynamic response analysis. III. A consistency filter and application to four northern elephant seal colonies. Marine Mammal Science 4:210–222.

Breiwick, J. M., E. D. Mitchell and D. G. Chapman. 1981. Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: an iterative method. Fishery Bulletin (U.S.) 78:843–853.

Breiwick, J. M., L. L. Eberhardt and H. W. Braham. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Sciences 41:484–496.

Cooke, J. G. 1986. On the net recruitment rate of gray whales with reference to interspecific comparisons. Reports of the International Whaling Commission 36:363–366.

DeMaster, D. P. 1981. Incorporation of density dependence and harvest into a general population model for seals. Pages 389–401 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

DeMaster, D. P. 1984. A review of density dependence in marine mammals. Proceedings of the Workshop on Biological Interactions among Marine Mammals and Commercial Fisheries in the Southeastern Bering Sea. Alaska Sea Grant Report 84-1, pp. 139–148.

DeMaster, D. P., D. J. Miller, D. Goodman, R. L. DeLong and B. S. Stewart. 1982.

Assessment of California sea lion fishery interactions. Transactions of the 47th North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C. pp. 253–264.

EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205–212.

EBERHARDT, L. L., D. G. CHAPMAN AND J. R. GILBERT. 1979. A review of marine mammal census methods. Wildlife Monographs 63, 46 pp.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

FAY, F. H., B. P. KELLY AND J. L. SEASE. 1989. Managing the exploitation of Pacific walruses: a tragedy of delayed response and poor communication. Marine Mammal Science 5:1–16.

FOWLER, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602–610.

FOWLER, C. W. 1984. Density dependence in cetacean populations. Pages 373–379 *in* W. F. Perrin, R. L. Brownell, Jr. and D. P. DeMaster, eds. Reproduction in whales, dolphins and porpoises. Reports of the International Whaling Commission, Special Issue 6.

FOWLER, C. W. 1988. Population dynamics as related to rate of increase per generation. Evolutionary Ecology 2:197–204.

GERRODETTE, T. 1987. A power analysis for detecting trends. Ecology 68:1364–1372.

GERRODETTE, T. 1988. Dynamic response analysis. II. Evaluation of dynamic response analysis in a simulated no-harvest case. Marine Mammal Science 4:196–209.

GILPIN, M. E., T. J. CASE AND F. J. AYALA. 1976. θ-selection. Mathematical Biosciences 32:131–139.

GOODMAN, D. 1988. Dynamic response analysis. I. Qualitative estimation of stock status relative to maximum net productivity level from observed dynamics. Marine Mammal Science 4:183–195.

GULLAND, J. A. 1987. Seals and fisheries: a case for predator control? Trends in Ecology and Evolution 2:102–104.

HARWOOD, J., AND J. P. CROXALL. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. Marine Mammal Science 4:13–33.

HOLT, S. J., AND L. M. TALBOT. 1978. New principles for the conservation of wild living resources. Wildlife Monographs 59, 33 pp.

KENYON, K. W. 1969. The sea otter in the eastern Pacific Ocean. U.S. Fish and Wildlife Service, North American Fauna 68. [Also Dover Publications, New York, NY, 1975, 352 pp.]

LANDER, R. H., ed. 1980. Summary of northern fur seal data and collection procedures. NOAA Technical Memorandum NMFS-F/NWC-3, 162 pp.

LANKESTER, K., AND J. R. BEDDINGTON. 1986. An age structured population model applied to the gray whale (*Eschrichtius robustus*). Reports of the International Whaling Commission 36:353–358.

MARINE MAMMAL COMMISSION. 1986. Annual report of the Marine Mammal Commission, calendar year 1985. A report to Congress. Marine Mammal Commission, Washington, D.C., 180 pp.

OHSUMI, S. 1976. Population assessment of the California gray whale. Reports of the International Whaling Commission 26:350–359.

REILLY, S. B. 1981. Population assessment and population dynamics of the California gray whale (*Eschrichtius robustus*). Ph.D. thesis, University of Washington, Seattle, WA. 279 pp.

REILLY, S. B., D. W. RICE AND A. A. WOLMAN. 1983. Population assessment of the gray whale, *Eschrichtius robustus,* from California shore censuses, 1967–80. Fishery Bulletin (U.S.) 81:267–279.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:1–382.

Smith, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin (U.S.) 81:1–13.

Smith, T. D., and T. Polacheck. 1979. Analysis of a simple model for estimating historical population sizes. Fishery Bulletin (U.S.) 76:771–779.

York, A. E. 1985. Estimation of numbers of pups born on St. Paul Island during 1977 and 1978. Pages 16–18 *in* P. Kozloff, ed. Fur seal investigations, 1982. NOAA Technical Memorandum NMFS-F/NWC-71.

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Demographic Consequences of Changed Pupping and Hauling Sites of the Hawaiian Monk Seal

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Abstract: *During the last 30 years, changes in the size of Hawaiian monk seal populations at several locations have been associated with the amount and type of human disturbance. Recreational beach activities caused monk seals to alter their pupping and hauling patterns. Survival of pups in suboptimal habitats was low, leading to gradual population declines. During the last decade at Kure Atoll, the process has been reversed: human disturbance on beaches has decreased, and traditional pupping and hauling sites have been reestablished. Subsequently, high survival rates of young seals, coupled with two successful enhancement programs for female pups, have led to dramatic changes in the age and sex composition of the population. Based on these changes, the monk seal population at Kure Atoll soon should begin to increase. Apparently small behavioral changes in such vital activities as feeding and reproduction can have large demographic consequences. Therefore, monitoring of endangered species should include data on habitat use and age and sex composition, as well as estimates of abundance.*

Resúmen: *Durante los últimos treinta años, los cambios en el tamaño de las poblaciones de la foca de Hawai en varias localidades, han sido asociados con la cantidad y el tipo de perturbación humana. Las actividades recreativas en las playas causaron que las focas alteraran su patrones de procreación y alimentación. La sobrevivencia de los cachorros en habitats subóptimos fué muy baja originando la disminución gradual de las poblaciones. Durante la última década, en Kure Atoll, el proceso ha sido revertido: la perturbación humana en las playas ha disminuido y los lugares tradicionales de procreación y alimentación han sido reestablecidos. Subsecuentemente, los altos indices de sobrevivencia de las focas jóvenes, aparejados con dos exitosos programas para acrecentar los cachorros hembra, han producido cambios dramáticos en la composición, en edad y sexo, de la población. Basado en estos cambios, la población de la foca de Hawai en Kure Atoll deberia de empezar a incrementarse pronto. Los cambios aparentemente pequeños en actividades vitales como la alimentación y la reproducción pueden tener grandes consecuencias demográficas. Por lo tanto, el monitoreo de las especies en peligro debe de incluir datos sobre el uso del hábitat y la composición en cuanto a la edad y el sexo así como cálculos estimados sobre la abundancia.*

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> "The primary cause of the decay of organic diversity is not direct human exploitation or malevolence, but the habitat destruction that inevitably results from the expansion of human populations and human activities" (Ehrlich 1988)

It is widely recognized that anthropogenic destruction of habitat is a leading cause of the loss of species diversity on Earth. Clearing of rain forests and draining of wetlands are obvious examples, but "destruction" of habitat also can be more subtle. It need not involve physical alteration of habitat. Seemingly benign human activities can cause small but important changes in a species' behavior that, by their demographic effects, can have major population consequences. This is clearly demonstrated by the recent history of Hawaiian monk seals (*Monachus schauinslandi*).

With few exceptions, Hawaiian monk seals live and breed only in the Northwestern Hawaiian Islands (Kenyon & Rice 1959; Kenyon 1981), a 1800-km string of small, mostly uninhabited islands forming the northwestern end of the Hawaiian Archipelago. The Hawaiian Islands National Wildlife Refuge includes most of the range of the Hawaiian monk seal. Because of an apparently low rate of migration between islands (Johnson & Kridler 1983), monk seals form somewhat discrete populations at eight islands or atolls. Following a general population decline in the 1960s and 1970s, the species was declared endangered in 1976 under provisions of the U.S. Endangered Species Act (Gilmartin 1983).

A particularly sharp decline has occurred in the monk seal population at Kure Atoll (28°25′N, 178°10′W), which lies at the northwestern end of the Hawaiian chain. Beach counts of adult seals declined from over 100 in the late 1950s to about 30 in the late 1970s to less than 14 in the late 1980s (Table 1). The number of pups born at Kure Atoll similarly declined from about 30 per year to 10 and then to a mean of 5 during the same period (Table 1). A low point was reached in 1986 when only a single pup was born.

The following account of the decline of monk seals and their potential recovery at Kure Atoll draws on seal counts and observations over several decades. Numerous beach counts of monk seals have been made annually at Kure Atoll since 1981 by the National Marine Fisheries Service (NMFS) using a uniform methodology. Earlier counts by various researchers at less regular intervals used procedures that varied somewhat. Because the number of seals hauled out varies by time of day and time of year, in this report we have made pre-1981 data comparable by selecting only beach counts begun between 1200 and 1500 hours of each day and 1 March and 30 September of each year. Unless noted otherwise, seal counts include all seals counted on the beach except pups of the year.

Causes of the Decline

The emergent land at Kure Atoll consists of a single, permanent, vegetated island, Green Island, and several much smaller sand islets. Before human occupation, Green Island was the favored site for pupping and hauling out. The number of seals hauling out on Green Island declined after 1960 when the U.S. Coast Guard (USCG) built a loran station there (Fig. 1). Dogs and recreational beach activities of the 20–25 men at the station, primarily beachcombing for Japanese glass fishing floats, caused the seals to abandon the preferred Green Island beaches and haul out on the sand islets instead (Kenyon 1972). The converse effect has been observed on Tern Island at French Frigate Shoals, a multi-island atoll 1,350 km to the southeast. For more than two decades while a loran station was in operation on Tern Island, few seals were ever seen, but the number of seals using the island increased sharply after the USCG vacated the station in 1979 (Fig. 1). In 1988, the highest of the weekly seal counts on Tern Island was 118, and the March–September mean was 61.4.

The immediate effect of human beach activity on the choice of monk seal hauling sites is thus clear, but the

Table 1. Numbers of pups born, mean adult beach counts, and relative pupping rates (ratio of pups to adult beach count) at Kure Atoll for selected years, 1957–1988 (* = incomplete pup count; ** = single adult beach count).

Year	*Number of pups born*	*Mean adult beach count*	*Relative pupping rate*	*Reference*
1957	23*	79**	0.29	Kenyon & Rice 1959
1958	25*	107**	0.23	Rice 1960
1964	32			Wirtz 1968
1965	30			Wirtz 1968
1977	10	31.0	0.32	Johnson et al. 1982*a*
1978	10	33.0	0.30	Rauzon 1978
1985	5	14.1	0.35	Reddy & Griffith 1988
1986	1	11.5	0.09	NMFS unpublished data
1987	6	11.8	0.51	Reddy 1989
1988	8	13.1	0.61	Henderson & Finnegan 1990

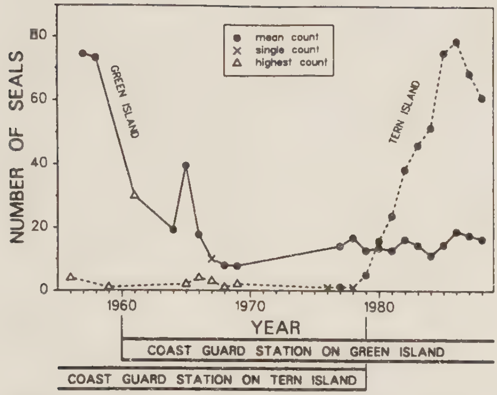

*Figure 1. Number of Hawaiian monk seals hauled out on Green Island, Kure Atoll, and Tern Island, French Frigate Shoals, 1956–1988. Filled circles indicate a mean count, triangles a maximum of several counts, and x's a single count. The U.S. Coast Guard built a loran station on Green Island in 1960 and vacated a loran station on Tern Island in 1979. The U.S. Fish and Wildlife Service took over the Tern Island station in 1979 and has operated it as a field research station since. (Sources: Svihla 1957; Udvardy & Warner 1964; Amerson 1971; Kenyon 1972; Schulmeister 1981; DeLong et al. 1976; Fiscus et al. 1978; Rauzon 1978; Johnson et al. 1982*b*; *Gilmartin 1983; Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS unpublished data.)*

demographic effects of changed pupping and hauling sites are less obvious and require a longer time to express themselves. In the absence of human disturbance, seals use the optimal sites available for their activities; a change to suboptimal sites may lead to higher mortality, lower fecundity, or both. After the establishment of the loran station on Green Island in 1960, fecundity, as indicated by number of pups per adult, did not decline (Table 1). However, pup mortality was very high (Wirtz 1968), and few immature seals were seen (Johnson et al. 1982*a*). There are no data on nonpup mortality rates. The virtual lack of immature seals, together with the steady decline in beach counts and number of births over several decades, is consistent with the hypothesis, first advanced by Kenyon (1972), that changed pupping and hauling sites lead to high postnatal mortality, low recruitment, and a gradually senescent population.

Several proximate causes of high postnatal mortality in Hawaiian monk seals are probable. First, preferred pupping sites have a calm nearshore area where pups, which are weak swimmers, develop their swimming ability (Westlake & Gilmartin 1990); however, the sand islets at Kure Atoll change size and shape frequently, and large waves may wash over them entirely. At other locations, we have observed pups swept out to sea and not returning. Second, sharks, especially large tiger sharks (*Galeocerdo cuvier*), are common near shore during the seal pupping season, apparently attracted by fledging albatross (*Diomedea immutabilis* and *D. nigripes*) chicks, which are unable to fly out of the water after swimming offshore or landing in the water. Shark predation is indicated by wounds on seals (Kenyon 1973), seal remains in shark stomachs (Taylor & Naftel 1978), and direct observation (Balazs & Whittow 1979; Alcorn & Kam 1986; Johanos & Kam 1986; Johanos & Austin 1988). Pupping locations on Green Island have shallow nearshore waters that probably offer some protection from sharks, but the sand islets do not.

Finally, the phocid pattern of maternal care makes the postnatal period a particularly vulnerable stage in the life cycle. Phocids (true seals) have a high rate of energy transfer from mother to pup during a short nursing period, terminated by an abrupt weaning (Oftedal et al. 1987). Hawaiian monk seal pups nurse for 35–40 days, during which the mother is in constant attendance to her pup and does not feed. The amount of energy transferred to the pup during the nursing period is critical since, after weaning, the pup must live on its fat reserves until it learns to feed on its own. Immature survival rates are positively correlated with weaning size in the Hawaiian monk seal (unpublished data) and other phocids (Coulson & Hickling 1964; Hill 1987). Repeated interruption or stress during the nursing period reduces the amount of milk the pup receives and its subsequent likelihood of survival. Disruption of normal maternal care has been a factor in the decline of many threatened and endangered mammals (Oldfield 1988).

Similar factors related to human disturbance have altered monk seal population sizes at two other atolls, Midway Islands and French Frigate Shoals, although data are less complete than at Kure Atoll. Midway Islands became an active U.S. naval base in the early 1940s. If monk seals there reacted to human activity as they did at Kure Atoll, the seal decline was well under way when the first detailed counts were made in the late 1950s (Kenyon & Rice 1959). The rate of abortions, stillbirths, and preweaning deaths was a very high 46% at that time (Rice 1960). By the late 1960s, only a few seals were seen (Kenyon 1972), a situation that continues to the present. Thus, the monk seal decline at Midway Islands apparently took about 25–30 years, the same length of time as the decline at Kure Atoll and, not coincidentally, about the apparent lifespan of these seals (Kenyon 1981; unpublished data).

On the other hand, the monk seal population at French Frigate Shoals increased substantially between the late 1950s and the late 1970s (Johnson et al. 1982*a*), a puzzling anomaly against the general decline at most locations during this period. However, the increase makes sense if we consider the pattern of human disturbance. The primary pupping site at French Frigate Shoals is East Island (Westlake & Gilmartin 1990). A USCG loran station was located on East Island from 1944 to 1952 (Amerson 1971). East Island is much smaller than Green Island, and the disruption of pupping was undoubtedly greater. The loran station was moved to Tern Island in 1952, and monk seals avoided that location until the station ceased operation in 1979 (Fig. 1). Because Tern Island is not used for pupping, it is possible that pupping at the atoll returned to nearly normal once human activity around East Island stopped. Thus, the 1956–1958 seal counts at French Frigate Shoals were probably made at a low point, and with decreased human disturbance at the primary pupping island, the population recovered over the next two decades. The lack of juvenile and subadult seals at French Frigate Shoals in 1958 and the high proportion of them in 1977 (Johnson et al. 1982*a*) are consistent with this explanation.

Monk seal populations have declined at other locations in the Northwestern Hawaiian Islands (Johnson et al. 1982*a*), where human activity has been less intense. All of the islands, however, have suffered various degrees of human disturbance from a combination of shipwrecks; visits by fishermen; military activity; scientific research, including collections; and, in the more distant past, sealers, turtle hunters, guano miners, and seabird egg and feather collectors (Amerson 1971; Woodward 1972; Amerson et al. 1974; Clapp & Kridler 1977; Clapp et al. 1977; Ely & Clapp 1973; Clapp & Wirtz 1975). Other known sources of mortality include disease (Gilmartin et al. 1980), shark predation (Alcorn & Kam 1986), adult male aggression (Johnson & Johnson 1981; Johanos et al. 1987; Alcorn 1984; Johanos & Austin 1988), and entanglement in debris (Henderson 1984, in press). Data are insufficient to assess the relative contribution of these sources of mortality to the population declines at the other islands.

Changes Leading to Recovery

After the Hawaiian monk seal was declared an endangered species in 1976, management actions were undertaken to assist its recovery. The USCG modified its regulations at Kure Atoll to reduce disturbance to seals. Dogs were banned from the station, recreational driving of vehicles on the beaches was eliminated, and seal refuge areas with restricted access were established at the north end of Green Island and on the sand islets. The immediate effects of these changes on seal behavior are difficult to quantify since no data are available from the early 1970s. The biggest documented changes occurred after 1981, when NMFS began an annual research program there. Seals began pupping on Green Island again (Fig. 2); in fact, since 1982, 33 of the 35 births at Kure Atoll have occurred on Green Island. Also, seals once again began using Green Island as the main haul-out area (Fig. 2). The fraction of seals presently using Green Island for hauling out (about 0.60–0.65) is far above the figure of 0.16 recorded in 1968 when disturbance was high, but is still below the figure of 0.72 in the late 1950s before the station was built (Kenyon 1972). The fraction of seals using Green Island is significantly higher after 1980 for both hauling out ($P < 0.05$) and pupping ($P < 0.005$, rank-sum test, two-tailed). We believe these changes in the seals' behavior result from changes in the behavior and attitude of USCG personnel toward monk seals; the latter changes, in turn, result from (1) restrictions on beach activities beginning in 1976; and (2) an increased awareness of and concern for the plight of the monk seals beginning in 1981, coincident with the NMFS research presence.

Beach counts have indicated that there are about three adult male seals for each adult female at Kure Atoll. The reasons for this excess of males, which also occurs at some but not all other locations, are a current focus of research. Because of the declining number of females and the unbalanced sex ratio, two programs aimed at increasing the number of female seals were initiated in recent years at Kure Atoll. The first project, "Headstart," was begun in 1981 and continues to the present. Female pups have been collected after weaning, tagged on the rear flippers, and placed in a large (ca. 40

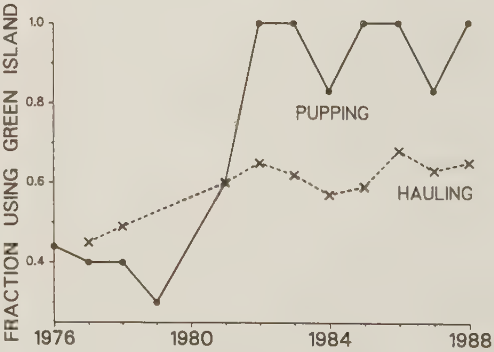

*Figure 2. Fraction of Hawaiian monk seals at Kure Atoll using Green Island for pupping (●) and hauling (x), 1976–1988. (Sources: DeLong et al. 1976; Fiscus et al. 1978; Rauzon 1978; Rauzon et al. 1978; Johnson et al. 1982*a*; Johnson et al. 1982*b*; Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS unpublished data.)*

m × 60 m) fenced beach enclosure with equal areas of sand and water (Gilmartin et al. 1986). The enclosure is stocked with live fish trapped on nearby reefs. Female pups are kept in the enclosure throughout the summer months and released in September of each year, at 3–7 months of age. Male pups are similarly tagged after weaning but not placed in the enclosure. Survival rates from weaning to one year have been higher for the protected females (14/15 = 0.93) than for the unprotected males (14/17 = 0.82). The difference is not significant based on a chi-square test (= 0.05), but with this small sample, the probability of detecting such a difference is low (1 − <0.2) (Cohen 1988). The median annual survival rate of all seals from 1 to 4 years of age has been 0.94 (Gilmartin et al. 1987). These high survival rates since 1981, even for male pups not given the extra protection of the enclosure, coincide with the shifts in pupping and hauling sites (Fig. 2).

In the second program, begun in 1984 at French Frigate Shoals where the population is larger, severely underweight female pups are collected after weaning, treated and fed in Honolulu, and released as yearlings at Kure Atoll the following spring (Gilmartin & Gerrodette 1986). Six of the eight seals so treated and released through 1987 were alive at Kure Atoll in 1988, one had emigrated to Midway Islands, and one was not seen in 1988.

The female pup enhancement programs, while involving a small number of animals, have thus been extremely effective at a critical stage in the life cycle. Equally important, the shifts in pupping and hauling sites have resulted in high survival rates for all immature seals since 1981. The cumulative demographic effect on this small population has been substantial. Although the number of seals at Kure Atoll remains low, the decline has been halted. The total number of seals has not changed much since 1981, but a large shift in the age and sex composition has occurred (Fig. 3). Before 1981 immature seals (approximately ages 1–5 for females, 1–6 for males) were rarely seen; now they constitute half the population. Moreover, in contrast to adults, the sex ratio in the immature portion of the population is 2:1 in favor of females. The number of births is increasing after reaching a low of a single pup in 1986. All eight seals who gave birth at Kure Atoll in 1988 were identified; five of them are known to have first pupped in 1987 or 1988, a sixth first pupped in 1984, and the ages of the other two mothers are unknown. Because monk seals may live to 25 years or more, the breeding population as well as the total population is now quite young. The high pupping rates in 1987 and 1988 (Table 1) may be the result of a young and more fecund breeding population, but the sample sizes are small and the high pupping rates could have occurred by chance alone. In any case, if fecundity remains at least at its historical level and survival remains as high as it has been since 1981, the population soon should begin to increase.

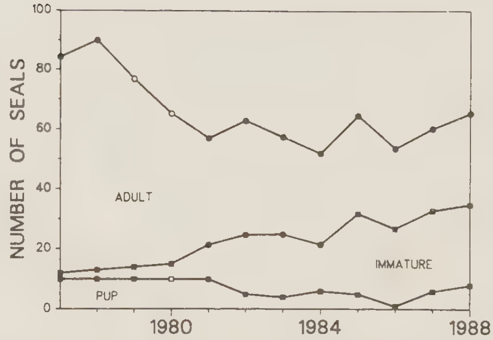

*Figure 3. Number of Hawaiian monk seals in each of three age categories at Kure Atoll, 1977–1988. Pups are seals born in that year; immatures are seals 1 year and older but less than adult size; adults are seals of full adult size or observed breeders. Squares indicate a completely known cohort of tagged or individually recognizable seals. Circles indicate number of seals estimated from a mean beach count based on the mean observed haul-out fraction of immature seals from 1985 to 1988. Open symbols indicate points estimated from partial data. (Sources: Rauzon 1978; Johnson et al. 1982*a*; *Johnson et al. 1982*b; *Gilmartin et al. 1986; Reddy & Griffith 1988; Reddy 1989; NMFS, unpublished data.)*

Conclusions

We are cautiously optimistic for growth of the monk seal population at Kure Atoll in the near future. The causes of the seals' decline were reversible, and the seals' responses to changes in human behavior have been dramatic and well documented. Monk seals and humans can coexist on these islands if humans do not disrupt the seals' vital activities of hauling out, pupping, and feeding. This has been clearly demonstrated by the seals' increased use of Tern Island after 1979 when the USCG loran station was replaced by a USFWS field station (Fig. 1; Schulmeister 1981). Under the USFWS, access to the beach at Tern Island, as well as elsewhere in the atoll, has been strictly limited to necessary research, and the researchers make special efforts to avoid disturbing the seals (USFWS 1986).

Our findings have applications to a related endangered species, the Mediterranean monk seal (*M. monachus*). That species is declining rapidly in abundance, and exists only as small scattered colonies around islands in the Mediterranean Sea and eastern subtropical

Atlantic Ocean (Sergeant 1984). Habitat loss, pollution, and shootings by fishermen are thought to be primary causes of the decline, but indirect human effects may be operating as well, as in the Hawaiian case. It is clear from their remaining distribution in only the most remote locations that Mediterranean monk seals avoid human activity. Because of this avoidance, the seals may be using suboptimal pupping, hauling, and feeding sites. In the past, the Mediterranean monk seal apparently used sandy beaches (Ronald & Yeroulanos 1984), as the Hawaiian species does, but now hauling and pupping are confined to caves. Lower fecundity and survival rates at such sites could be contributing to the population decline. On the positive side, the success of the Hawaiian monk seal pup relocation program from French Frigate Shoals to Kure Atoll has shown that seals will tend to remain at a new location if moved when young and held in semicaptivity before release. If sanctuary areas with suitable habitat could be identified for the Mediterranean monk seal (Avella 1984; Biscoito 1984; Ronald & Yeroulanos 1984), it might be possible to establish or increase populations at these sanctuaries by moving young seals from areas where conflicts with humans are a problem.

The case of the Hawaiian monk seal at Kure Atoll also has lessons for monitoring endangered species in general. First, monitoring should include more than estimates of population size. Estimating population size (or an index of population size) over time is a necessary but insufficient condition for monitoring. Factors that indicate the condition of a population can alert wildlife managers to incipient problems at an earlier stage (Eberhardt & Siniff 1977; Gerrodette & DeMaster 1990). Such factors could include individual physiological condition (growth rate, size, weight, and disease), behavioral observations (mating, nesting, feeding, and social interactions), and demographic characteristics of the population (age, stage, size, and sex composition). The decline of the monk seal population at Kure Atoll would have been detected earlier if, for example, the size composition of the population had been recorded as well as total seal count. Even today, after more than a decade of effort at restoring the population, total counts of monk seals at Kure Atoll have not changed very much. Our optimism for the future growth of the population comes from a more detailed consideration of the changing age and sex structure of the population (Fig. 3).

Second, monitoring requires a long-term commitment. Many "charismatic" endangered species are characterized by long lives and low rates of reproduction. For animals and plants with such life histories, changes in population size may occur slowly—excepting, of course, catastrophic mortality or rapid habitat destruction. Changes in the monk seal population at Kure Atoll are clear from the perspective of several decades, but less clear at other locations where fewer counts have been made.

Third, a species' habitat may be made unsuitable in subtle ways. Recent declines of Hawaiian monk seals in the presence of humans were not caused by malevolence or even by habitat alteration in the usual sense. Apparently benign human activities caused small behavioral changes that had large population effects. Beachcombing, jogging, and similar activities may have seemed innocuous, yet there is little question that Hawaiian monk seals would have been extirpated at Kure Atoll had changes not been made. Every species requires suitable habitat to carry out its vital activities, and the denial of access to such critical habitat kills as surely as direct exploitation.

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Literature Cited

Alcorn, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Department of Commerce, NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC-**42.** 37 pp.

Alcorn, D. J., and A. K. H. Kam. 1986. Fatal shark attack on a Hawaiian monk seal (*Monachus schauinslandi*). Marine Mammal Science **2:**313–315.

Amerson, A. B., Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Research Bulletin **150.** 383 pp.

Amerson, A. B., Jr., R. B. Clapp, and W. O. Wirtz II. 1974. The natural history of Pearl and Hermes Reef, Northwestern Hawaiian Islands. Atoll Research Bulletin **174.** 306 pp.

Avella, J. 1984. A plan for the reintroduction of the monk seal (*Monachus monachus*) in the Archipelago of Cabrera, Balearic Islands, Spain. Pages 92–101 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Sociéte des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.

Balazs, G. H., and G. C. Whittow. 1979. First record of a tiger shark observed feeding on a Hawaiian monk seal. 'Elepaio 39:107–109.

Biscoito, M. 1984. On the creation of a natural reserve in the Desertas Islands, Madeira—Portugal. Pages 88–91 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Sociéte des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.

Clapp, R. B., and E. Kridler. 1977. The natural history of Necker Island, Northwestern Hawaiian Islands. Atoll Research Bulletin **206.** 102 pp.

Clapp, R. B., E. Kridler, and R. R. Fleet. 1977. The natural history of Nihoa Island, Northwestern Hawaiian Islands. Atoll Research Bulletin **207.** 147 pp.

Clapp, R. B., and W. O. Wirtz II. 1975. The natural history of Lisianski Island, Northwestern Hawaiian Islands. Atoll Research Bulletin **186.** 196 pp.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Publishers, Hillsdale, New Jersey.

Coulson, J. C., and G. Hickling. 1964. The breeding biology of the grey seal, *Halichoerus grypus* (Fab.), on the Farne Islands, Northumberland. Journal of Animal Ecology **33:**485–512.

DeLong, R. L., C. H. Fiscus, and K. W. Kenyon. 1976. Survey of monk seal (*Monachus schauinslandi*) populations of the Northwestern (Leeward) Hawaiian Islands. Northwest Fisheries Center Processed Report. 36 pp.

Eberhardt, L. L., and D. B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada **34:**183–190.

Ehrlich, P. R. 1988. The loss of diversity: causes and consequences. Pages 21–27 in E. O. Wilson and F. M. Peter, editors. Biodiversity. National Academy Press, Washington, D.C.

Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Research Bulletin **171.** 361 pp.

Fiscus, C. H., A. M. Johnson, and K. W. Kenyon. 1978. Hawaiian monk seal (*Monachus schauinslandi*) survey of the Northwestern (Leeward) Hawaiian Islands, July 1978. Northwest and Alaska Fisheries Center Processed Report. 27 pp.

Gerrodette, T., and D. P. DeMaster. 1990. Quantitative determination of optimum sustainable population level. Marine Mammal Science **6:**1–16.

Gilmartin, W. G. 1983. Recovery plan for the Hawaiian monk seal, *Monachus schauinslandi.* U.S. Department of Commerce, NOAA, National Marine Fisheries Service, Southwest Region, Terminal Island, California. Various paging.

Gilmartin, W. G., R. L. DeLong, A. W. Smith, L. A. Griner, and M. D. Dailey. 1980. An investigation into unusual mortality in the Hawaiian monk seal, *Monachus schauinslandi*. Pages 32–41 in R. W. Grigg and R. T. Pfund, editors. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24–25, 1980, University of Hawaii, Honolulu, Hawaii. UNIHI-SEAGRANT-MR-80-**04**.

Gilmartin, W. G., and T. Gerrodette. 1986. Hawaiian monk seal population status and recovery potential at Kure Atoll. Southwest Fisheries Center Honolulu Laboratory, Honolulu, HI. Southwest Fisheries Center Administrative Report H-86-**16**. 26 pp.

Gilmartin, W. G., T. C. Johanos, and T. Gerrodette. 1987. Preliminary assessment of juvenile Hawaiian monk seal survival. Southwest Fisheries Center Honolulu Laboratory, Honolulu, HI. Southwest Fisheries Center Administrative Report H-87-**16**. 11 pp.

Gilmartin, W. G., R. J. Morrow, and A. M. Houtman. 1986. Hawaiian monk seal observations and captive maintenance project at Kure Atoll, 1981. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service. NOAA-TM-NMFS-SWFC-**59**. 9 pp.

Henderson, J. R. 1984. Encounters of Hawaiian monk seals with fishing gear at Lisianski Island, 1982. Marine Fisheries Review **46:**59–61.

Henderson, J. R. In press. Recent entanglements of Hawaiian monk seals in marine debris. Second International Conference on Marine Debris, Honolulu, Hawaii.

Henderson, J. R., and M. R. Finnegan. 1990. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi,* and captive maintenance project at Kure Atoll, 1988. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFSC-150. 23 p.

Hill, S. E. B. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. Ph.D. thesis. University of Minnesota, 106 pp.

Johanos, T. C., and S. L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-**118**. 38 pp.

Johanos, T. C., and A. K. H. Kam. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-**58**. 37 pp.

Johanos, T. C., A. K. H. Kam, and R. G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-**70**. 38 pp.

Johnson, A. M., R. L. DeLong, C. H. Fiscus, and K. W. Kenyon. 1982*a*. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. Journal of Mammalogy **63:**415–421.

Johnson, A. M., and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. 'Elepaio **44:**43–45.

Johnson, A. M., J. Ruehle, K. W. Kenyon, and M. Rauzon. 1982*b*. Hawaiian monk seal studies, summary report, 1977–1980. Unpublished report. 76 pp. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).

Johnson, B. W., and P. A. Johnson. 1981. The Hawaiian monk seal on Laysan Island: 1978. U.S. Department of Commerce, National Technical Information Service, PB82-109661. 17 pp.

Kenyon, K. W. 1972. Man versus the monk seal. Journal of Mammalogy **53**:687–696.

Kenyon, K. W. 1973. Hawaiian monk seal (*Monachus schauinslandi*). Pages 88–97 in proceedings of a working meeting of seal specialists on threatened and depleted seals of the world, held under the auspices of the Survival Service Commission, 18–19 August 1972, at the University of Guelph, Ontario, Canada. International Union for Conservation of Nature and Natural Resources, 1110 Morges, Switzerland.

Kenyon, K. W. 1981. Monk seals *Monachus* Fleming, 1822. Pages 195–220 in S. H. Ridgway and R. J. Harrison, editors. Handbook of marine mammals. Volume 2: Seals. Academic Press, London, England.

Kenyon, K. W., and D. W. Rice. 1959. Life history of the Hawaiian monk seal. Pacific Science **13**:215–252.

Oftedal, O. T., D. J. Boness, and R. A. Tedman. 1987. The behavior, physiology, and anatomy of lactation in the Pinnipedia. Pages 175–245 in H. H. Genoways, editor. Current Mammalogy. Volume 1. Plenum Press, New York.

Oldfield, M. L. 1988. Threatened mammals affected by human exploitation of the female-offspring bond. Conservation Biology **2**:260–274.

Rauzon, M. J. 1978. Hawaiian monk seal studies at Kure Atoll, 8 March to 19 April 1978. Unpublished report. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).

Rauzon, M. J., K. W. Kenyon, and A. M. Johnson. 1978. Observations of monk seals, French Frigate Shoals, 17 February to 27 May 1977. Unpublished report. (Available from Marine Mammals and Endangered Species Program, National Marine Fisheries Service Honolulu Laboratory, 2570 Dole St., Honolulu, HI 96822).

Reddy, M. L. 1989. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi,* and captive maintenance project for female pups at Kure Atoll, 1987. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-**123**. 37 pp.

Reddy, M. L., and C. A. Griffith. 1988. Hawaiian monk seal population monitoring, pup captive maintenance program, and incidental observations of the green turtle at Kure Atoll, 1985. U.S. Department of Commerce, NOAA Technical Memorandum, National Marine Fisheries Service, NOAA-TM-NMFS-SWFC-**101**. 35 pp.

Rice, D. W. 1960. Population dynamics of the Hawaiian monk seal. Journal of Mammalogy **41**:376–385.

Ronald, K., and M. Yeroulanos. 1984. A conservation plan for *Monachus monachus* on Greek islands and coasts. Pages 31–40 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Sociéte des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.

Schulmeister, S. 1981. Hawaiian monk seal numbers increase on Tern Island. 'Elepaio **41**:62–63.

Sergeant, D. E. 1984. Review of new knowledge of *Monachus monachus* since 1978 and recommendations for its protection. Pages 21–30 in K. Ronald and R. Duguy, editors. Les phoques moines—monk seals, proceedings of the Second International Conference on the Monk Seals. Annales de la Sociéte des Sciences Naturelles de la Charente-Maritime. Supplement. December 1984.

Svihla, A. 1957. Observations on French Frigate Shoals, February 1956. Atoll Research Bulletin **51.** 2 pp.

Taylor, L. R., and G. Naftel. 1978. Preliminary investigations of shark predation on the Hawaiian monk seal at Pearl and Hermes Reef and French Frigate Shoals. U.S. Department of Commerce, National Technical Information Service, PB-285-626. 34 pp.

Udvardy, M. D. F., and R. E. Warner. 1964. Observations on the birds of French Frigate Shoal and Kure Atoll. Atoll Research Bulletin **103.** 3 pp.

U.S. Fish and Wildlife Service. 1986. Hawaiian Islands National Wildlife Refuge, Master plan/environmental impact statement. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Region One. Various paging.

Westlake, R. L., and W. G. Gilmartin. 1990. Hawaiian monk seal pupping locations in the Northwestern Hawaiian Islands. Pacific Science **44**:366–383.

Wirtz, W. O., II. 1968. Reproduction, growth and development, and juvenile mortality in the Hawaiian monk seal. Journal of Mammalogy **49**:229–238.

Woodward, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. Atoll Research Bulletin **164**. 318 pp.

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Iridoteuthis iris (Cephalopoda: Sepiolidae): New Records from the Central North Pacific and First Description of the Adults[1]

Robert F. Harman[2] and Michael P. Seki[3]

ABSTRACT: *Iridoteuthis iris* (Berry, 1909) was originally described from a unique specimen collected in the main Hawaiian Islands, but the holotype is no longer extant. New material was collected from the southern Emperor–northern Hawaiian Ridge seamounts, extending the known range of *I. iris* by about 3200 km. The new samples are described, including the first description of adults.

The species composition of the cephalopod fauna around the Hawaiian Archipelago is well known relative to that of many other areas. Some species records, however, are from unique specimens and/or juvenile individuals. Such is the case with the sepiolid *Iridoteuthis iris* (Berry, 1909), which was described from a single juvenile collected from the steamer *Albatross* near the island of Molokai in the main Hawaiian Islands.

Iridoteuthis iris has remarkably large fins and eyes, a huge ventral shield, and a broad dorsal commissure between the head and mantle. Berry (1909) originally named the species *Stoloteuthis iris*, based on similarities to *S. leucoptera* from the Atlantic. Naef (1912) thought the species was different enough from *Stoloteuthis* to be placed in a new genus, *Iridoteuthis*, basing his decision largely on the size and shape of the fins, the broad dorsal commissure and nuchal fold, and the large head and eyes. In his monograph of the Hawaiian cephalopods, however, Berry (1914) stood by his original designation, but kept *Iridoteuthis* as a subgenus. This taxonomic uncertainty remained because the animal described by Berry (1909) was small and presumed to be a juvenile. The holotype is no longer extant (Sweeney et al. 1988), and the species was not seen again until 1984, when another individual was collected in Mamala Bay off the island of Oahu (ca. 60 km from the type location) in a bottom dredge from the vessel *Janthina*. This specimen was photographed (Figure 1) and subsequently lost (B. Burch, per. comm., Honolulu).

Recently, a series of cruises to the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts by the Southwest Fisheries Center Honolulu Laboratory aboard the NOAA ship *Townsend Cromwell* produced 45 of these sepiolids, including juveniles and adults. This report provides the first description of the adults and extends the known range of *Iridoteuthis iris* by about 3200 km, from the Hawaiian Islands to the southern Emperor seamounts.

DISTRIBUTION

The material was collected during six cruises from March 1978 to June 1986 at four seamounts in the SE–NHR: Southeast (SE) and Northwest (NW) Hancock, Colahan, and Kammu seamounts (Figure 2). These seamounts lie 2400 to 3200 km northwest of the type location. The summit depths range from 260 m at SE Hancock to 350 m at Kammu. Collections were made with several types of open trawls, including a Marinovich herring trawl, Isaacs-Kidd midwater trawl (IKMT), Cobb pelagic trawl, and Nor'Eastern bottom trawl. Target sampling depths over the seamount ranged from 73 to 305 m. Sampling was also conducted in waters away from the seamount during two cruises to SE Hancock

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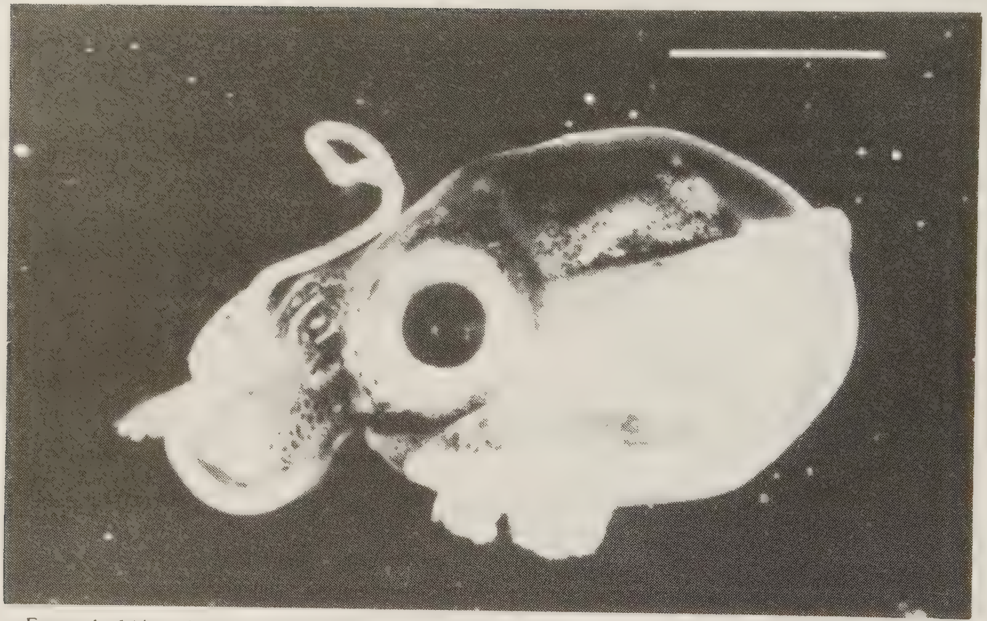

FIGURE 1. *Iridoteuthis iris* collected off Oahu, Hawaii, in 1984. Scale bar = 10.0 mm. (Photo by T. Burch.)

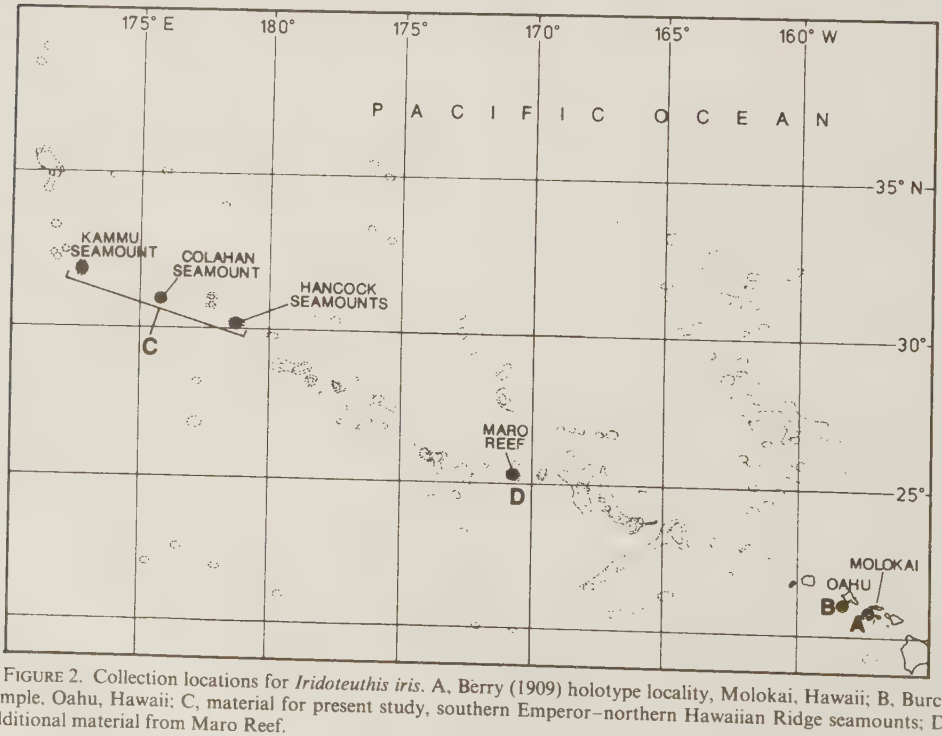
175° E
180°
175°
170°
165°
160° W
PACIFIC OCEAN
35° N
30°
25°
KAMMU SEAMOUNT
COLAHAN SEAMOUNT
HANCOCK SEAMOUNTS
C
MARO REEF
D
MOLOKAI
OAHU
B
A

FIGURE 2. Collection locations for *Iridoteuthis iris*. A, Berry (1909) holotype locality, Molokai, Hawaii; B, Burch sample, Oahu, Hawaii; C, material for present study, southern Emperor–northern Hawaiian Ridge seamounts; D, additional material from Maro Reef.

TABLE 1

Iridoteuthis iris: Material Examined and Capture Data

MANTLE LENGTH (mm)	SEX	CRUISE	STATION	DATE	LAT. (°N)	LONG. (°E)	SEAMOUNT	TIME	GEAR	MAXIMUM DEPTH FISHED (m)
5.5	—	TC 85-01	122	14 Feb. 1985	29.48.1	179.05.2	SE Hancock	0400	IKMT	238
6.0	—	TC 85-01	139	15 Feb. 1985	29.49.0	179.04.0	SE Hancock	2018	IKMT	209
6.5	—	TC 85-01	130	14 Feb. 1985	29.48.0	179.02.9	SE Hancock	2035	IKMT	218
6.9	—	TC 84-05	114	23 July 1984	29.47.0	179.06.0	SE Hancock	2241	IKMT	209
7.0	—	TC 85-01	139	15 Feb. 1985	29.49.0	179.04.0	SE Hancock	2018	IKMT	209
7.0	—	TC 85-01	139	15 Feb. 1985	29.49.0	179.04.0	SE Hancock	2018	IKMT	209
7.9	—	TC 82-05	58	18 Oct. 1982	31.02.2	175.51.7	Colahan	1016	Nor'Eastern	291
7.9	F	TC 85-01	119	13 Feb. 1985	29.47.3	179.03.5	SE Hancock	2256	IKMT	236
8.0	M	TC 86-06	63	11 Feb. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
8.0	M	TC 86-06	63	11 Feb. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
8.5	M	TC 84-05	104	21 July 1984	29.48.6	179.04.4	SE Hancock	2209	IKMT	225
8.5	F	TC 83-03	5	15 Aug. 1983	31.57.4	173.07.8	Kammu	2245	Cobb	150
8.5	M	TC 86-06	63	11 Feb. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
9.5	M	TC 83-03	5	15 Aug. 1983	31.57.4	173.07.8	Kammu	2245	Cobb	150
9.5	F	TC 85-01	123	14 Feb. 1985	29.47.9	179.02.2	SE Hancock	0503	IKMT	218
10.0	F	TC 85-01	119	13 Feb. 1985	29.47.3	179.03.5	SE Hancock	2256	IKMT	236
10.0	M	TC 86-06	63	11 Feb. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
10.0	F	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
10.5	F	TC 83-03	5	15 Aug. 1983	31.57.4	173.07.8	Kammu	2245	Cobb	150
10.5	F	TC 84-05	104	21 July 1984	29.48.6	179.04.4	SE Hancock	2209	IKMT	225
10.5	M	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
10.7	F	TC 83-03	5	15 Aug. 1983	31.57.4	173.07.8	Kammu	2245	Cobb	150
11.0	F	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
11.0	F	TC 84-05	114	23 July 1984	29.47.0	179.06.0	SE Hancock	2241	IKMT	209
11.1	M	TC 82-05	58	18 Oct. 1982	31.02.2	175.51.7	Colahan	1016	Nor'Eastern	291
11.2	F	TC 85-01	130	14 Feb. 1985	29.48.0	179.02.9	SE Hancock	2035	IKMT	218
11.5	M	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
11.5	M	TC 86-06	63	11 Feb. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
11.5	F	TC 84-05	93	16 July 1984	29.47.7	179.06.2	SE Hancock	2051	IKMT	150
12.0	M	TC 84-05	94	16 July 1984	29.48.1	179.05.7	SE Hancock	2239	IKMT	220
13.0	F	TC 84-05	104	21 July 1984	29.48.6	179.04.4	SE Hancock	2209	IKMT	225
13.2	M	TC 83-03	5	15 Aug. 1983	31.57.4	173.07.8	Kammu	2245	Cobb	150
13.8	F	TC 86-05	96	8 Sept. 1986	29.48.0	179.01.9	SE Hancock	0202	Marinovich	230
15.0	M	TC 85-03	138	14 July 1985	29.47.8	179.01.7	SE Hancock	0029	Marinovich	245
15.2	F	TC 86-05	96	8 Sept. 1986	29.48.0	179.01.9	SE Hancock	0202	Marinovich	230
15.5	F	TC 84-05	114	23 July 1984	29.47.0	179.06.0	SE Hancock	2241	IKMT	209
18.5	M	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
18.9	M	TC 85-01	132	14 Feb. 1985	29.48.1	179.03.0	SE Hancock	2330	IKMT	216
19.5	M	TC 86-06	63	11 Oct. 1986	29.46.5	179.03.6	SE Hancock	2059	Marinovich	202
21.3	F	TC 85-01	119	13 Feb. 1985	29.46.5	179.03.6	SE Hancock	2256	IKMT	236
21.7	M	TC 78-03	31	9 Sept. 1978	30.16.5	178.42.3	NW Hancock	1324	Nor'Eastern	300
24.1	M	TC 85-01	132	14 Feb. 1985	29.46.5	179.03.6	SE Hancock	2330	IKMT	216
25.5	F	TC 82-05	58	18 Oct. 1982	31.02.2	175.51.7	Colahan	1016	Nor'Eastern	291
28.4	F	TC 82-05	58	18 Oct. 1982	31.02.2	175.51.7	Colahan	1016	Nor'Eastern	291
30.0	F	TC 82-05	58	18 Oct. 1982	31.02.2	175.51.7	Colahan	1016	Nor'Eastern	291

Seamount. No sepiolids were taken in the latter tows, indicating that *Iridoteuthis iris* belongs with other seamount-associated species, such as the lightfish, *Maurolicus muelleri*, and the lophogastrid mysid, *Gnathophausia longispina* (Boehlert 1988). Table 1 presents the material examined and summarizes the capture data.

Recently, three additional specimens were collected near Maro Reef (25°22.4′ N, 170°20.1′ W) in the Northwestern Hawaiian Islands. Maro Reef is closer than the seamounts to the type location in the main islands, about 1400 km to the southeast.

DESCRIPTION

All samples were fixed in 10% formalin in seawater, subsequently preserved in 50% isopropanol, and then measured. The measurements are based on Roper and Voss (1983) and are diagrammed in Figure 3. Table 2 contains representative measurements of the morphometric parameters for 10 adults. Morphometric indices were computed by dividing each measurement by the corresponding dorsal mantle length (ML). Material has been deposited in the U.S. National Museum of Natural History, Washington, D.C. (museum numbers 817136 to 817138).

Body (Figure 4) short and muscular; mantle rounded at posterior end; pronounced bulge medially on dorsal mantle; dorsal commissure between head and mantle broad, extending to near lateral midpoint of eye; ventral mantle with large shield (about 80% ventral mantle length), which nearly covers funnel and eyes from below; shield with anterior medial indentation; large, internal photophore with two large internal pores. *Head* broad and short, dominated by large eyes with circular lids that overlap the cornea all around. The morphometric indices for the head and body are summarized in Table 3. *Funnel* large and sometimes swollen near tip; funnel organ trilobed, accessory pads oval, locking apparatus smooth, groove oval but slightly curved and broader at anterior end.

Fins very large; rounded-oblong with pointed posterior margins; base small relative to fin length; plane of attachment nearly medial on lateral surface of mantle. The morphometric indices for the fins are summarized in Table 3.

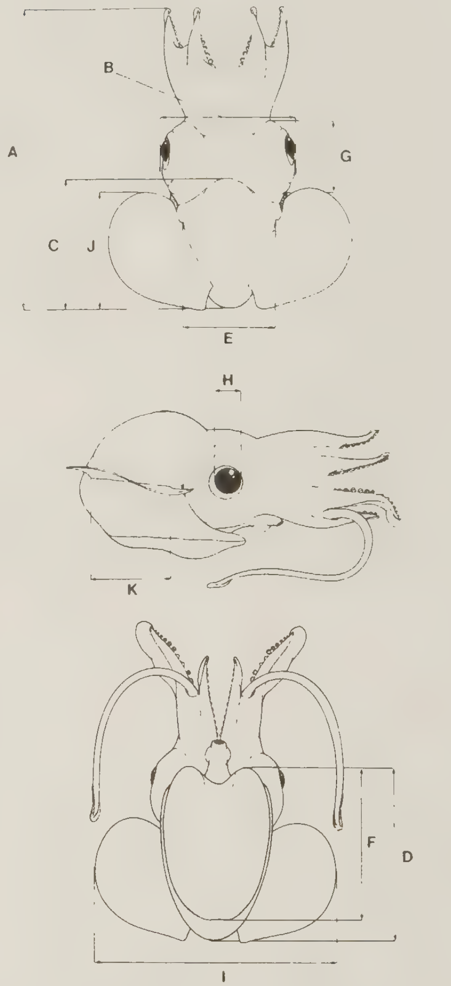

FIGURE 3. Location of *Iridoteuthis iris* measurements. A, total length; B, head width; C, dorsal mantle length; D, ventral mantle length; E, mantle width; F, shield length; G, eye diameter; H, eye lens diameter; I, fin width; J, fin length; K, fin base length. Measurements of arms and tentacles were made on oral surface from beak to arm or tentacle tip.

TABLE 2

Iridoteuthis iris: REPRESENTATIVE ADULT MEASUREMENTS

PARAMETERS MEASURED	MEASUREMENTS OF MALES (mm)					MEASUREMENTS OF FEMALES (mm)				
Dorsal mantle length	8.5	10.5	11.5	15.5	24.1	9.5	11.0	13.0	15.5	28.4
Total length	19.5	33.5	31.0	41.0	60.1	24.0	24.5	28.5	32.0	46.6
Head width	12.5	15.5	14.5	18.0	20.2	13.5	14.6	15.0	17.3	17.4
Ventral mantle length	13.0	18.0	20.0	24.5	30.0	13.5	16.9	20.0	21.5	29.8
Mantle width	7.0	10.0	11.0	13.5	16.2	7.5	9.4	10.5	11.4	15.0
Shield length	11.5	15.0	17.0	20.5	24.8	12.3	14.4	17.0	20.9	26.9
Eye diameter	7.5	10.5	11.0	13.5	15.7	6.7	9.5	10.0	11.5	14.5
Eye lens diameter	3.0	3.5	3.0	4.4	4.5	2.5	1.7	3.5	2.0	3.4
Fin width	26.5	29.5	28.5	37.0	42.5	21.3	23.5	29.0	32.1	36.0
Fin length	12.5	16.0	16.0	19.0	21.8	12.4	13.5	16.5	17.7	18.4
Fin base	6.0	6.5	8.0	19.5	12.2	6.2	6.9	7.0	8.4	7.7
Tentacle club length	4.5	4.0	5.0	6.5	7.1	3.5	4.0	6.0	6.0	9.5
Tentacle length	21.0	30.0	29.0	26.0	41.5	11.0	26.0	35.0	31.0	51.8
Length arm I	6.0	5.5	14.0	19.5	23.2	7.5	7.5	9.0	10.3	13.9
Length arm II	6.0	5.5	14.0	19.5	23.3	8.0	7.5	9.0	10.4	15.5
Length arm III	7.5	8.5	15.0	22.5	28.2	9.0	7.5	10.0	13.8	14.9
Length arm IV	6.0	4.5	11.0	15.0	20.1	8.0	7.9	9.5	11.4	16.3

Tentacles long and slender; stalk bare; tentacular organ (keel) present on aboral margin of stalk, just proximal to club. *Tentacle club* (Figure 5) diameter slightly greater than stalk, with two distinct sucker fields; distal half covered with crowded, minute suckers numbering 14–25 ($\bar{x} = 19.1 \pm 2.4$ SD) across; number of suckers independent of body size from at least 8 mm ML; proximal suckers slightly larger and less dense, numbering 6–14 ($\bar{x} = 10.7 \pm 1.7$ SD) across; no obvious sexual dimorphism. Figure 5 shows scanning electron micrographs of large and small suckers from the club of an 11.5-mm ML individual; the outer ring is composed of flattened plates surrounded by a toothless border, and the inner ring bears several knobs.

Arms (Figure 6) short and muscular; extensive web present between all but ventral pairs; all arms with aboral keels that may over-reach arm tips in males; male arm formula III > I ≃ II > IV, female and juvenile arm formula III > I ≃ II ≃ IV; armature consists of biserial globular suckers bearing smooth rings; suckers on short pedicels; marginal trabeculae sometimes present; sexual dimorphism obvious in individuals larger than about 8 mm ML; protective membranes more developed in females. Table 3 summarizes the arm length indices. A more detailed description of armature in *I. iris* larger than 8 mm ML follows:

Arm I.	Male:	20 to 28 suckers ($\bar{x} = 24.4 \pm 2.5$); suckers present at arm tips; one series (7–9 suckers) relatively reduced distally.
	Female:	18 to 32 suckers ($\bar{x} = 28.3 \pm 3.3$); no suckers on arm tips.
Arm II.	Male:	22 to 31 suckers ($\bar{x} = 25.1 \pm 1.9$); proximal two-thirds with 10–14 suckers (slightly enlarged toward middle of arm) and distal third with 12–16 smaller ones.
	Female:	24 to 45 suckers ($\bar{x} = 39.0 \pm 4.9$), largest at base and decreasing gradually to tip.
Arm III.	Male:	24 to 31 suckers ($\bar{x} = 27.1 \pm 2.5$); dorsal series with several greatly enlarged suckers in middle portion of arm, proximal to "naked" region bearing only short pedicels, no suckers; 12–15 suckers proximal to naked area and 9–16 distal; aboral keel greatly enlarged.

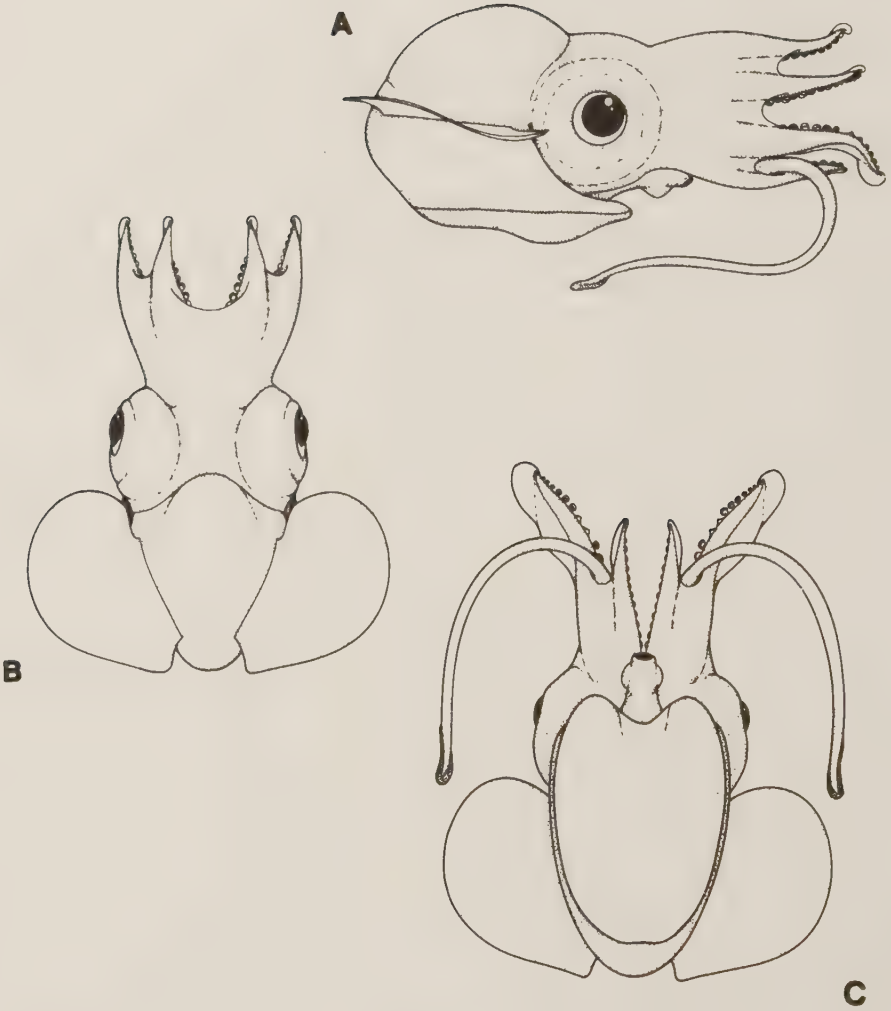

FIGURE 4. *Iridoteuthis iris* male, 24.1 mm dorsal mantle length. (*A*) lateral; (*B*) dorsal; (*C*) ventral.

Female: 18 to 27 suckers ($\bar{x} = 22.0 \pm 2.3$); proximal two-thirds with suckers, ending distally at small naked area; distal third with elongate trabeculae only.

Arm IV. Male: 80 to 106 suckers ($\bar{x} = 94.1 \pm 8.2$); proximal half of arm with 10–20 relatively large suckers; distal half with 70+ small, crowded suckers in four rows.

Female: 14 to 55 suckers ($\bar{x} = 29.3 \pm 7.9$); proximal half of arm with 6–14 relatively large suckers; next quarter with 10–30 smaller suckers in somewhat regular rows; distal portion bears trabeculae.

TABLE 3

SUMMARY OF MORPHOMETRIC INDICES FOR *Iridoteuthis iris* (MINIMUM-*MEAN*-MAXIMUM)

MORPHOMETRIC PARAMETERS	TOTAL ($n = 45$) (5.5–30.0 mm ML)	MALE ($n = 18$) (8.0–24.1 mm ML)	FEMALE ($n = 21$) (7.9 30.0 mm ML)	JUVENILE ($n = 7$) (5.5–7.0 mm ML)
Mantle width	0.5-*0.8*-1.4	0.6-*0.9*-1.4	0.5-*0.8*-1.1	0.6-*0.8*-0.9
Ventral mantle length	1.0-*1.4*-1.8	1.2-*1.5*-1.8	1.0-*1.4*-1.8	1.1-*1.3*-1.5
Shield length	0.8-*1.3*-1.5	0.9-*1.3*-1.5	0.8-*1.2*-1.5	0.8-*1.1*-1.3
Head width	0.6-*1.2*-2.1	0.7-*1.2*-2.1	0.6-*1.2*-1.9	1.0-*1.2*-1.4
Eye diameter	0.5-*0.7*-1.0	0.6-*0.8*-1.0	0.5-*0.7*-1.0	0.6-*0.7*-0.7
Eye lens diameter	0.1-*0.2*-0.4	0.1-*0.3*-0.4	0.1-*0.2*-0.4	0.2-*0.2*-0.3
Fin width	1.3-*2.1*-3.1	1.6-*2.3*-3.1	1.3-*2.1*-2.8	2.0-*2.1*-2.4
Fin length	0.6-*1.2*-1.7	0.9-*1.2*-1.5	0.6-*1.2*-1.7	1.1-*1.2*-1.5
Fin base	0.3-*0.6*-1.3	0.4-*0.6*-1.3	0.3-*0.6*-1.2	0.5-*0.6*-0.6
Arm I	0.2-*0.7*-1.3	0.2-*0.8*-1.3	0.3-*0.6*-0.9	0.4-*0.5*-0.6
Arm II	0.2-*0.7*-1.3	0.2-*0.8*-1.3	0.3-*0.6*-0.9	0.4-*0.5*-0.6
Arm III	0.4-*0.8*-1.5	0.5-*1.0*-1.5	0.4-*0.7*-0.9	0.5-*0.6*-0.7
Arm IV	0.4-*0.7*-1.0	0.4-*0.7*-1.0	0.4-*0.7*-0.9	0.4-*0.6*-0.7

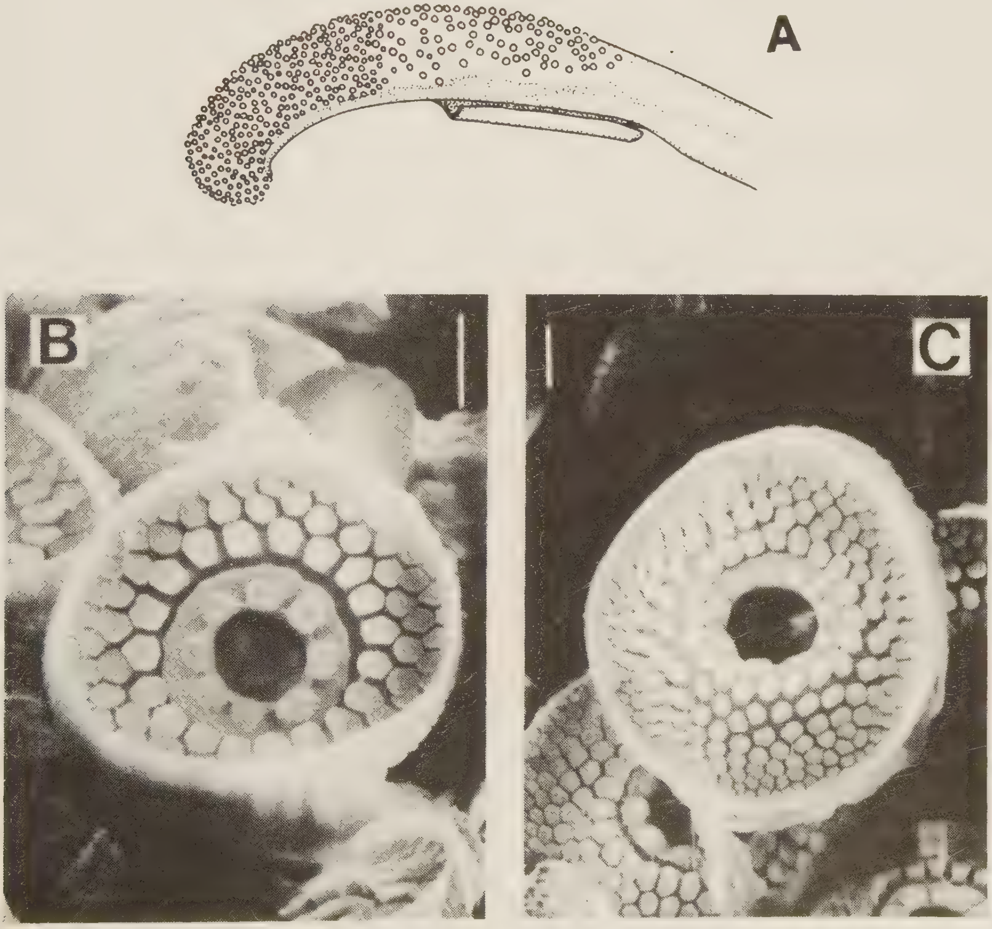

FIGURE 5. Tentacle club from *Iridoteuthis iris*. (*A*) 24.1 mm dorsal mantle length (ML). Scanning electron micrographs of suckers from 11.5-mm ML individual (scale bar = 10 μm): (*B*) from distal field of small suckers; (*C*) from proximal field of large suckers.

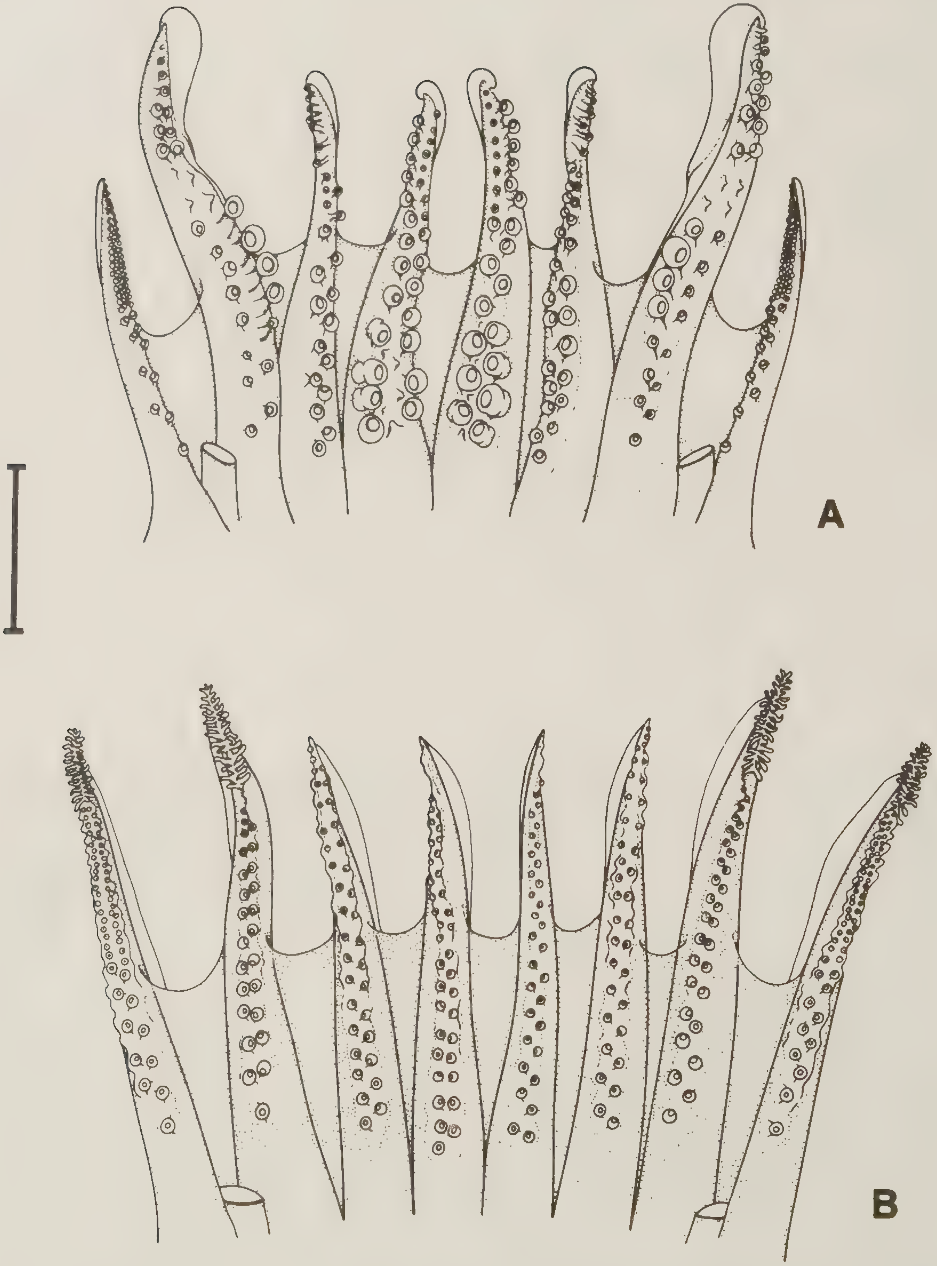

FIGURE 6. Oral views of *Iridoteuthis iris* arms. (*A*) 24.1-mm dorsal mantle length (ML) male; (*B*) 21.3-mm ML female. Dorsal arms are central. Scale bar = 5.0 mm.

DISCUSSION

The only other named species of this genus is *Iridoteuthis maoria* (Dell 1959) from the South Pacific. As in *I. iris*, this species has a broad dorsal mantle commissure and large middorsal bulge on the mantle, as well as very large eyes, ventral shield, and pointed fins; these may be valid generic characters. *Iridoteuthis maoria* males that we examined, however, had relatively smaller aboral keels on the arms than did male *I. iris*, and most of the enlarged suckers were on the second arms with a few on the third arms, the reverse of *I. iris*. The right dorsal arm of *I. maoria* is much thicker than the left, whereas in *I. iris* the dorsal arms are similar. In addition, the tentacle club suckers of *I. maoria* are relatively less numerous and dense.

We have compared the new material with *Stoloteuthis leucoptera* and agree with Naef's (1912) suggestion that this species is, indeed, different enough to be placed in *Iridoteuthis*. *Iridoteuthis* alone has a large middorsal bulge on the mantle, and relatively larger eyes and ventral shield than *Stoloteuthis*. In *Stoloteuthis*, unlike *Iridoteuthis*, the dorsal mantle commissure is relatively narrow, the males do not have greatly developed aboral keels on the third arms, there is no clear size difference between suckers on the tentacular clubs, and the fins are roughly semicircular and do not reach the posterior end of the mantle. In addition, male *Stoloteuthis* have only a few enlarged suckers on one set of arms, the second, whereas *Iridoteuthis* have enlarged suckers on the second and third arms, as well as other sexual dimorphism.

The identity of the new material remains tentative. Based solely on Berry's (1909) description and photographs taken of the individual collected off Oahu, the new samples from the SE-NHR seamounts appear to be identical to *Iridoteuthis iris*. Positive identity, however, must await further collections closer to the type locality in the main Hawaiian Islands.

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LITERATURE CITED

BERRY, S. S. 1909. Diagnosis of new cephalopods from the Hawaiian Islands. Proc. U.S. Natl. Mus. 37:407–419.

———. 1914. The cephalopoda of the Hawaiian Islands. Bull. Bur. Fish. 32:255–362.

BOEHLERT, G. W. 1988. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems. GeoJournal 16(1): 45–52.

DELL, R. K. 1959. Some additional New Zealand cephalopods from Cook Strait. Zool. Publ. Victoria Univ. Wellington 25: 1–12.

NAEF, A. 1912. Teuthologische Notzien. 3. Die Arten der Gattungen *Sepiola* und *Sepiella*. Zool. Anz. 39(7): 262–271.

ROPER, C. F. E., and G. L. VOSS. 1983. Guidelines for taxonomic descriptions of cephalopod species. Pages 49–63 *in* Roper et al., eds. Memoirs of the National Museum of Victoria 44.

SWEENEY, M. J., C. F. E. ROPER, and F. G. HOCHBERG. 1988. A catalogue of the type specimens of recent Cephalopoda described by S. Stillman Berry. Malacologia 29(1): 7–19.

On Measuring Fishing Fleet Productivity: Development and Demonstration of an Analytical Framework

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Abstract.–This study develops and demonstrates a framework for measuring changes in the total-factor productivity of fishing fleets operating in common-property, open-access fisheries. This approach is distinguished from previous efforts to measure productivity growth in fisheries by our explicit treatment of the fishery resource as a constraint on production and by the incorporation of recent advances in productivity measurement that take into account variations in the degree of capacity utilization in an industry. The approach is developed in sufficient detail for the non-economist fishery analyst to follow and implement. The empirical analysis of total-factor productivity growth in the U.S. tropical tuna fleet reveals that this approach eliminates a significant amount of bias in fleet productivity measures which is otherwise introduced when using traditional methods of productivity analysis.

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Measuring changes in productivity has long been an important component in evaluating an industry's economic performance. Such measures in fishing industries can signal the need for, as well as indicate the success of, policy or management actions. Measurement of productivity growth or technical progress in marine fishing industries has received attention by Bell and Kinoshita (1973), Davis et al. (1987), Duncan (n.d.), Kirkley (1984), and Norton et al. (1985).

Two considerations not addressed by previous researchers are important for evaluating productivity growth in fishing industries. First, traditional measures of productivity implicitly assume that a fishing industry's capital stock is being utilized, in an economic sense, at its long-run equilibrium or capacity output level. Thus, traditional measures fail to adjust for variations in the degree of utilization of the industry's productive capacity. Second, the effect of changes in abundance of the fish stock on productivity growth in fishing industries has not been specifically accounted for in the traditional analysis. As a result, changes in resource abundance are not disentangled from changes in productivity.

In this study we develop a nonparametric framework utilizing the method of growth accounting and economic index numbers to analyze the productivity growth of fishing fleets operating in common-property, open-access fisheries. The framework is then demonstrated by analyzing productivity growth in the U.S. tropical tuna purse seine fleet over the years 1981–1985.[1] We also demonstrate a method for deriving implicit aggregate output and input price indices for the purse seine fleet.

In developing the productivity assessment framework, we introduce further refinements to the standard procedure described by Denny et al. (1981) and Cowing et al. (1981)—which has seen continual improvement since the pioneering work of Solow (1957)—by adjusting for variations in capacity utilization and changes in resource abundance. The exposition includes the technical detail necessary to provide the non-economist fishery analyst with a comprehensible and useful means of tracking and analyzing productivity growth and performance in fisheries.

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[1] The method is non-parametric because parameters of the production technology or production function are not econometrically estimated. The method of growth accounting and economic index numbers is discussed in a later section of the text. Econometric estimation of productivity growth does not impose the conditions of a constant-returns-to-scale production technology and Hicks-neutral technical change. However, this comes at the expense of more demanding data requirements: either a longer time-series of aggregate data or more vessel-level observations in any given year. In addition, some fairly sophisticated econometrics and economics are required to estimate and interpret the results.

In the following section we introduce the methodology used to analyze total factor productivity in fishing fleets. The potential bias from failing to account for variation in economic capacity utilization is investigated in the third section. We discuss the data, empirical issues, and the construction of index numbers for the U.S. tropical tuna purse-seine fleet in the fourth section, and then we develop the implicit price indices and report and interpret results of the empirical analyses in the fifth section.

Total-factor productivity

The standard procedure for estimating total-factor productivity is derived from the economic theory of production. In common-property natural resource industries, the production function expresses a stock-flow relationship between the resource stock and the flow of resource extraction or output from the production activity in any given time-period. An important consideration when measuring productivity growth in fishing industries is defining the role of the common-property resource stock in the production technology.

Rather than treating the common-property resource as a conventional input (Scott 1954, Clark 1976, Dasgupta and Heal 1979), it is more appropriately specified as a constraint to the production technology. The fish stock is a biological constraint on the production technology because its abundance affects the production environment within which fishing firms operate, but it is beyond the control of any individual firm. That is, the use of conventional inputs such as capital, labor, and energy is conditional upon expected resource-abundance levels. Changes in resource abundance shift the production technology. McFadden (1978) develops this approach by treating environmental parameters (such as resource abundance) in a manner similar to disembodied technical change; i.e., technological progress due to more efficient use of existing inputs. Finally, resource abundance is a technological constraint because the total catch cannot exceed the abundance available, and an increase (decrease) in resource abundance allows an increase (decrease) in catch for any given level of input usage and state of technology.[2]

When the fish stock is treated as a technological constraint, the production function, F, relates the maximum flow of output in time t (such as tons of fish extracted), $Y(t)$, to the flow of $N+1$ inputs, $X_1(t)$, $X_2(t),\ldots,X_{N+1}$, the state of technology represented by $A(t)$,[3] and abundance of the fish stock indexed by $B(t)$:

$$Y(t) = F[X_1(t), X_2(t),\ldots,X_{N+1}(t); A(t), B(t)]. \quad (1)$$

Growth-accounting framework

Total-factor productivity measures are derived from equation (1) using the growth-accounting framework and economic index numbers.[4] This approach accounts for the growth in output flow over time by partitioning this output growth among the growth in inputs, technical progress, and changes in resource stock abundance. Total-factor productivity is then measured as the residual in the growth of output flow after accounting for all of the measurable sources of growth.

Under the growth-accounting framework, a constant-returns-to-scale production function is assumed, so that a proportional increase in inputs yields a proportional increase in output flow for any given level of resource stock abundance and state of technology. Movement in time t is assumed to lead to improvements in the state of technology, so that $\delta F/\delta A(t)>0$ (Solow 1957). Following conventional practice, we further assume a particular form of technological change, Hick's-neutral disembodied technical change.[5] Moreover, $\delta F/\delta B(t)>0$, so that increases (decreases) in resource stock-size allow an increase (decrease) in the flow rate of extraction for any given input bundle and state of technical progress. We assume a Schaefer (1957)-type production technology, and further assume that changes in resource stock-size are Hick's neutral, so that the proportions with which all inputs are used remain constant for any given level of resource stock abundance.

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[2] Gordon (1954) similarly treated biological abundance as a technological constraint. Gordon (p. 136) states, "For each given level of population, a larger fishing effort will result in larger landings. Each population contour is, then, a production function for a given population level." Moreover, as Gordon noted, this approach does not preclude the impact that increases in catch typically have in reducing the resource stock. If resource abundance was instead another factor of production, like labor or capital, then changes in resource abundance would imply movements along the existing production function rather than shifts up or down the production function.

[3] The state of technology refers to the current level of technology or kind of production process utilized. For example, the current state of technology in the U.S. tuna fleet is represented by purse seining with some level of usage of vessel electronics.

[4] For a discussion of some of the limitations to the growth-accounting approach to measuring total-factor productivity, see Nelson (1981).

[5] Technological change or progress refers to the changes in a production process that come from the application of knowledge. These changes in the production process can be realized in various ways: through improved methods of utilizing existing resources, such that a higher catch-rate per unit of input ("effort") is obtained for a given level of resource stock abundance, often referred to as disembodied technological change; through changes in input quality, referred to as embodied technological change; or through the introduction of new processes and new inputs, which can be either (or both) disembodied and embodied technological change.

Hick's neutral technological change, whether disembodied or embodied, means that the technological advance does not change the proportions in which different inputs are used. Thus, for example, after technological change, capital, labor, energy, and any other inputs would be combined in the same proportions as before.

The productivity growth-accounting measure is fully developed in the Appendix, while only its final form is presented here:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} S_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \tag{2}$$

where the dots over variables represent time derivatives, $S_i(t) = P_i(t)X_i(t)/P(t)Y(t)$; i.e., the income or cost share of input X_i, where $P_i(t)$ is the price of input X_i in time t, and $P(t)$ is the price of output Y in time t. Productivity growth $\dot{A}/A$ is the residual of output growth $\dot{Y}/Y$ after accounting for aggregate input growth $\Sigma_i S_i(\dot{X}_i/X_i)$ and changes in resource abundance $\dot{B}/B$. This index of total-factor productivity growth is also called a Divisia index.

Tornqvist economic index numbers

A convenient discrete-time approximation to the continuous Divisia index is provided by Tornqvist (1936). The Tornqvist discrete approximation to the Divisia index of total-factor productivity growth (*TFP*) is expressed as:

$$\begin{aligned} \frac{TFP_t}{TFP_{t-1}} &= \prod_{j=1}^{M} [Y_{jt}/Y_{j,t-1}]^{1/2(R_{jt}+R_{j,t-1})} \\ &\quad - \prod_{i=1}^{N+1} [X_{it}/X_{i,t-1}]^{1/2(S_{it}+S_{i,t-1})} \\ &\quad - \frac{B_t}{B_{t-1}}, \end{aligned} \tag{3}$$

where the Y_j are outputs, the X_i are the $N+1$ inputs, B is the index of resource abundance, the $R_j = P_jY_j/\Sigma_j P_jY_j$ are output revenue shares, and the S_i are $N+1$ input cost shares.[6] As the interval between time-periods approaches zero, discrete-time Equation (3) approaches continuous-time Equation (2).

Chain indices

We use the method of chain indices to calculate the Tornqvist total-factor productivity index. Chain indices directly compare adjacent observations in a sequence of economic index numbers.[7] Nonadjacent observations are only indirectly compared, using the intervening observations as intermediaries, a practice resulting in transitive comparisons. The general form of the chain index can be written:

$$\begin{aligned} TFP_{t,t+N}^{\text{chain}} &= TFP_{t,t+1} \cdot TFP_{t+1,t+2} \cdot \ldots \\ &\quad \cdot TFP_{t+N-1,t+N}, \end{aligned} \tag{4}$$

where each individual term of Equation (4), $TFP_{t,t+1}$, is computed by the bilateral Tornqvist formula given in Equation (3), and represents the change from time period t to time-period $t+1$; i.e., $TFP_{t,t+1} = TFP_{t+1}/TFP_t$.

Productivity and capacity utilization

If firms are in long-run equilibrium, quasi-fixed inputs are optimally utilized in that the total cost of production per unit of output is minimized. This long-run optimal utilization is called full economic capacity utilization. Under long-run equilibrium, the flow of services from a quasi-fixed input is assumed proportional to the stock of that input, so that the available services from each of the quasi-fixed inputs are fully utilized: the observed stocks replace unobserved service flows in Equation (2) (Berndt and Fuss 1986).

When quasi-fixed inputs are not optimally utilized, i.e., the firm is not in long-run equilibrium, the observed productivity growth is composed of both the true technical progress impact, captured by $\dot{A}/A$ in Equation (2), and the rate of change in capacity utilization. An additional source of output variation is added to Equation (3): variations in capacity utilization (*CU*). To develop this argument, suppose that the $N+1^{th}$ input is now a quasi-fixed input capital (*K*), while the first N inputs are variable inputs. Then growth in productivity is written as (Hulten 1986):

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N} S_i \frac{\dot{X}_i}{X_i} - S_K \left[\frac{\dot{CU}}{CU} + \frac{\dot{K}}{K} \right] - \frac{\dot{B}}{B}, \tag{5}$$

where S_K is capital's cost share.

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[6] In practice, the logarithmic form of Equation (3) is computed, which gives the productivity growth between two periods. The exponent of this computation is then taken to obtain $TFP_{t,t-1}$. These period-to-period changes are then typically chained as in Equation (4) to form the Tornqvist bilateral chain index. The logarithmic form of the Tornqvist index is:

$$\begin{aligned} \ln(TFP_t/TFP_{t-1}) &= 0.5 \sum_{j=1}^{M} (R_{jt} + R_{j,t-1}) \ln(Y_{jt}/Y_{j,t-1}) \\ &\quad - 0.5 \sum_{i=1}^{N+1} (S_{it} + S_{i,t-1}) \ln(X_{it}/X_{i,t-1}) \\ &\quad - \ln(B_t/B_{t-1}). \end{aligned}$$

[7] The alternative approach is that of fixed-base indices in which *TFP* in any time t is directly compared with *TFP* in the initial or base period. See Squires (1988) for an extensive discussion within fisheries.

Failure to capture this additional source of variation creates a potential bias in the true productivity residual, $\dot{A}/A$, which varies with the rate of capacity utilization.

Methods of capacity utilization adjustment

When the firm is in temporary or short-run equilibrium rather than long-run equilibrium, the productivity residual formula can be adjusted for variations in *CU* in two different ways. The first relaxes the assumption that service flows are proportional to stocks by adjusting the stock of a quasi-fixed input to reflect its flow of services[8] (Berndt and Fuss 1986). Thus, rather than specifying capital as a stock (e.g., the number of vessels in the fleet), capital is measured by its flow of services or total time of utilization (e.g., as fleet vessel-days fished). Such a flow adjustment corresponds to an economic notion of CU, because we assume that a producer's decision to increase or decrease running and fishing time is the outcome of an economic optimization process.

The second approach to adjusting the productivity residual for *CU* variations uses engineering notions of the proportion of available productive capacity that is actually being utilized. Let capacity output Y^* represent the maximum possible output level corresponding to "normal" input usage, existing technology, and the stocks of quasi-fixed inputs. A measure of capacity utilization is then obtained by the identity: $CU \equiv Y/Y^*$, where Y is the observed output level.

Data and empirical issues

Tornqvist output indices for the U.S. tropical tuna purse-seine fleet were constructed using annual deliveries of skipjack and yellowfin tuna by the fleet to U.S. canneries and the corresponding dollar values of these deliveries. Weighted exvessel implicit prices for skipjack and yellowfin tuna were calculated by dividing the total dollar value of cannery receipts for each species by the total volume of cannery receipts. Revenue and cannery receipts data were obtained from the Southwest Region, National Marine Fisheries Service (NMFS). Dollar values were deflated by the GNP implicit price index.

To construct the input indices, four major categories of factors used in owning and operating a tropical tuna purse seiner were identified: labor, capital, fuel, and other intermediate inputs (transshipment services, repairs, gear, insurance, helicopter services, travel, and other). Constant-dollar unit prices for these inputs were estimated based on purse-seine expenditure data reported by the U.S. International Trade Commission (ITC 1986).

The labor index incorporates the flow of labor services derived by multiplying estimated total days absent (at sea or absent from port) per vessel per year by 19 crew members, which is the assumed average crew size in each year of the period. The unit price of labor, cost per crew-day-absent, was estimated by dividing the sum of the ITC's reported annual crew-related expenditures per vessel by a measure of annual crew-days-absent per vessel.

Three different capital indices were constructed for the total-factor productivity analysis of the U.S. tropical tuna fleet. The first two capital indices both assumed that firms were in long-run equilibrium and that the flow of capital services was proportional to the capital stock. The first capital index specified capital as the annual number of vessels in the fleet. The second capital index captured the effect of different vessel sizes (where size is a measure of the vessel's hold or carrying capacity) upon catch rates by measuring capital as the annual carrying capacity of the fleet.

The third capital index not only captured the effects of different-sized vessels, but also accounted for actual changes in the flow of services from this size-differentiated capital stock. In this third case, the flow of capital services was measured in annual ton-days-absent, an aggregation of each vessel's carrying capacity multiplied by the number of days it spent at sea during the year. Measures of annual ton-days-absent were derived from purse-seine-fleet activity data compiled by NMFS. The cost share for capital used in construction of all the capital indices was its market rental price, the sum of the annual interest expense and reported annual depreciation per vessel from the ITC sample.

The fuel index was constructed by dividing the annual fuel expenditure per vessel (from the ITC sample) by average fuel prices provided by the American Tuna Boat Association. Fuel consumption per vessel was then multiplied by the number of vessels in the fleet resulting in the aggregate annual fuel consumption.

The index of other intermediate inputs was derived by deflating the fleet's nominal expenditure on this category of inputs by the producer price index for industrial commodities. This approach represents the collective use of these inputs in real terms. The nominal expenditure for this category of inputs divided by the corresponding deflated expenditure was used as a proxy for the unit price of other intermediate inputs.

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[8] An alternative approach to accounting for variations in economic capacity utilization adjusts the cost or income shares rather than the flows of capital services. Berndt and Fuss (1986) and Hulten (1986) develop this approach, and Squires and Herrick (1988) provide a fisheries application. This approach is well suited when accurate and detailed data on running and fishing time are unavailable.

Table 1

Total-factor productivity growth in the U.S. tropical tuna fleet, 1981–85.

	No biomass adjustment				Biomass adjusted
	Capital input alternatives				
Period	No. of vessels[1]	Fleet carrying capacity[2]	Ton-days-absent[3]	Engineering-CU-adjusted carrying capacity[4]	Ton-days-absent; biomass adjustment[5]
1981–82	−0.1037	−0.1241	−0.0863	−0.1159	0.1006
1982–83	0.3739	0.3643	0.3378	0.1753	0.2120
1983–84	0.0298	0.0278	0.0767	0.1056	−0.4330
1984–85	0.0619	0.0499	0.0452	0.0932	0.0192
Mean	0.0905	0.0795	0.0933	0.0645	−0.0253

[1] Long-run equilibrium in capital, capital represented by the number of vessels; no biomass adjustment.
[2] Long-run equilibrium in capital, capital represented by fleet carrying capacity; no biomass adjustment.
[3] Capital input represented by the actual flow of capital services, ton-days-absent; no biomass adjustment.
[4] Capital represented by carrying capacity corrected for variations in capacity utilization (CU); no biomass adjustment.
[5] Capital represented by ton-days-absent; biomass adjusted.

Note: Calculated as Tornqvist bilateral indices using the logarithmic form of Equation (3) given in Footnote 6.

Because the U.S. tropical tuna purse-seine fleet operates almost exclusively in the Pacific Ocean, resource abundance measures relied on the extensive biological database that has been compiled by the Inter-American Tropical Tuna Commission (IATTC, La Jolla, CA 92038). From the IATTC database, we obtained estimates of annual yellowfin tuna biomass and estimates of catchability coefficients for yellowfin in the Commission's eastern tropical Pacific yellowfin regulatory area (CYRA). The CYRA was the only region of the Pacific for which such data were available. Moreover, there were no such data for skipjack tuna from any area of the Pacific. Because of these circumstances, it was not possible to explicitly account for fluctuations in biomass over the full range of the fishery and across all species harvested. Therefore, only the annual yellowfin biomass in the CYRA weighted by the catchability coefficient was used to adjust fleet productivity for changes in resource abundance.

Empirical results

Table 1 reports changes in annual total-factor productivity growth for the U.S. tropical tuna fleet over the period 1981–85 using Tornqvist bilateral-chain indices. Each of the total-factor productivity growth rates presented in Table 1 is distinguished by its specification of the capital input and adjustments for changes in resource abundance. Treatment of outputs and the other inputs is the same in all cases. To anticipate our results, we find that adjusting the traditional productivity measures for variations in economic capacity utilization and changes in resource abundance pares away sources of output growth that are not due to technical progress, giving a more accurate measure of productivity.

Productivity measures under full equilibrium

Columns (1) and (2) of Table 1 provide productivity growth measures assuming long-run equilibrium—economic capacity is fully utilized—without accounting for changes in resource abundance. The total factor productivity growth rates in column (1) use the first capital index: capital is represented by the number of vessels included in the fleet. The growth rates reported in column (2) are based on the second capital index: capital is represented by the carrying capacity of the fleet. Because vessels leaving the fleet during the period tended to be older and in the smaller size-categories, capital expressed in number of vessels decreased at a greater rate than capital measured in aggregate carrying capacity (columns [2] and [3] of Table 2). Hence, total-factor productivity growth based on the second capital index is lower than that based on the first capital index for those years in which the fleet declined.[9]

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[9] It might be argued that technical progress is embodied in the capital stock, so that different ages of vessels, embodying different advances in technical progress, should be explicitly considered. This is referred to as vintage effects, and is certainly the case for some types of technical progress such as purse seining versus pole-and-line harvesting. However, in recent years, much of the technical progress has been in the form of vessel electronics. While this type of technological change in a narrow sense, represents embodied technical change, so that vintage effects could theoretically be important, the volume of investment is negligible in comparison with the vessel's value, and much of the technical change is fundamentally related to the managerial function, information, and learning-by-doing: Hick's-neutral technical change.

Table 2

Annual growth in output, capital, CYRA* yellowfin tuna biomass, and capital stock capacity utilization rates, 1981–85.

Period	Output[1]	No. of vessels[2]	Fleet carrying capacity[3]	Ton-days-absent[4]	CYRA yellowfin tuna biomass[5]	Rate of capacity utilization[6]
1981–82	−0.0090	0.0947	0.1151	0.0773	−0.1869	−0.0327
1982–83	0.1869	−0.1870	−0.1774	−0.1508	0.1258	0.3898
1983–84	−0.0165	−0.0464	−0.0444	−0.0932	0.5096	−0.0244
1984–85	−0.0800	−0.1420	−0.1299	−0.1252	0.3167	−0.0125
Mean	0.0204	−0.0702	−0.0592	−0.0730	0.1913	0.0801

*Eastern tropical Pacific yellowfin regulatory area, IATTC.

[1] Annual change in deliveries of U.S.-caught yellowfin and skipjack tuna to U.S. canneries.

[2] Annual change in number of vessels comprising U.S. tropical tuna purse-seine fleet.

[3] Annual change in U.S. tropical tuna purse-seine fleet's hold capacity.

[4] Annual change in the fleetwide flow of capital services for the U.S. tropical tuna purse-seine fleet.

[5] Change in IATTC estimates of the annual CYRA yellowfin biomass.

[6] Annual change in ratio of actual U.S. tropical tuna purse-seine fleet output to fleet engineering capacity.

Note: In natural log form (cf. footnote 6).

Productivity measures adjusted for capacity utilization

The total-factor productivity growth rates presented in column (3) of Table 1 incorporate the third capital index: the annual flow of capital services from the size-differentiated capital stock, ton-days-absent. Since the number of ton-days-absent directly reflects the degree to which economic capacity is utilized, resulting measures of total-factor productivity growth are not subject to a capacity-utilization bias as are the growth rates shown in columns (1) and (2) of Table 1.

The effects of adjusting for *CU* are revealed in Table 2 by comparing the rates of change in the fleet's capital stock and the fleet's flow of capital services: fleet carrying capacity and ton-days-absent reported in columns (3) and (4), respectively. Between 1982 and 1983, fleet carrying capacity decreased 18%, while ton-days-absent decreased 15%. This means that the reduced fleet was fishing more intensively, and that a measure of productivity growth based on the stock of capital or fleet carrying capacity, without correcting for the degree of capacity utilization, will be biased upwards. Similarly, comparing growth in fleet carrying capacity and ton-days-absent between 1983 and 1984 reveals a greater decline in the latter relative to the former. Therefore, a smaller fleet capital stock is utilized (fished) proportionately less, and productivity growth based simply on the capital stock (carrying capacity) will be understated.

Column (4) of Table 1 reports growth in total factor productivity for the U.S. tropical tuna fleet, where changes in fleet carrying capacity—changes in the stock of capital—are corrected for variations in the rate of capacity-utilization. In this case, the capacity utilization adjustment is based on vessel design or engineering characteristics which act to establish an upper limit on fleet output in a physical sense. To estimate fleet engineering capacity, we assumed that each vessel was capable of making three fishing trips annually, filling its hold on each trip. Thus, maximum fleet output in each year is three times the fleet's carrying capacity. The ratio of actual fleet output (the total quantity of tuna delivered to canneries) to maximum potential fleet output estimates the degree of capacity utilization.

Changes in the rate of capacity utilization using the engineering adjustment are shown in column (6) of Table 2. These capacity-utilization rates were then used to derive the engineering-adjusted total-factor productivity growth rates presented in Table 1, column (4). Comparing the total-factor productivity growth rates in columns (2) and (4) of Table 1 discloses the extent of the bias introduced by failing to account for variations in the degree of capacity utilization.

The capacity-utilization adjustment is made to approximate the actual flow of services from the quasi-fixed factor, the capital stock. Therefore, one might expect the total-factor productivity growth rates using ton-days-absent (Table 1, column [3]) to closely correspond to those based on correcting for capacity utilization using the engineering approach (Table 1, column [4]). The fact that they do not points out that, in an economic sense, capacity-utilization adjustments explicitly recognize that quasi-fixed factors are not always utilized at the long-run equilibrium or full economic-capacity-output level, the level of output which minimizes the per-unit-cost of production. Under these circumstances, engineering-capacity output, as we have

Table 3

Implicit aggregate output and input price and total-factor-productivity chain indices.

Year	Total-factor productivity	Implicit aggregate output price	Implicit aggregate input price
1981	1.0000	1.0000	1.0000
1982	1.1058	0.9504	1.0221
1983	1.3669	0.8833	0.9016
1984	0.8865	0.7961	1.1941
1985	0.9037	0.7049	1.1099

Note: Implicit price indices formed by Fisher's weak factor-reversal relationship. See text for details. Total-factor productivity, calculated as Tornqvist bilaterial chain indices, adjusted for variations in biomass and capacity utilization (using ton-days-absent).

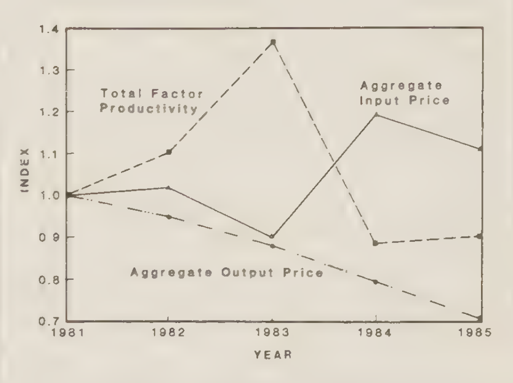

Figure 1

Total-factor productivity and implicit price indices.

defined it, should be greater than full economic-capacity output. Thus, the engineering capacity-utilization rates should be biased downward, and the corresponding productivity growth rates will inherit this bias. The preferred capacity-utilization correction, consistent with economic theory, should adjust the capital stock by its time in use to provide a flow measure of capital services.

Productivity measures adjusted for biological abundance

The total-factor productivity growth rates presented in column (5) of Table 1 are based on the actual flow of capital services and the growth of the yellowfin biomass in the CYRA (Table 2, column [5]). Comparing columns (3) and (5) of Table 1 indicates that the increase in the CYRA yellowfin biomass during most of the period acts to partially offset gains in total-factor productivity otherwise attributable to technical progress. The resource and capacity utilization adjusted total-factor productivity growth rates from Table 1, column (5) are used to compute the index of total factor productivity for the U.S. tropical tuna fleet shown in Table 3 and in Figure 1.[10]

Implicit output and input price indices

Fleet economic performance depends upon the real prices of outputs and inputs in addition to total-factor productivity. Corresponding to the aggregate output and input quantity indices are implicit aggregate output and input prices. These are calculated by a relationship due to Fisher (1922), which states that the product of the price index times the quantity index equals the expenditure ratio between the two time-periods. The implicit price index for an output (or input) can be interpreted as the ratio of the price level in period $t+1$ to the price level t. Fisher's relationship for the price (PI) and quantity (QI) indices for aggregate output Y can be written as:

$$PI(P_t,P_{t+1},Y_t,Y_{t+1})\,QI(P_t,P_{t+1},Y_t,Y_{t+1}) = \sum\nolimits_i P_{it+1}Y_{it+1}/\sum\nolimits_i P_{it}Y_{it}. \qquad (6)$$

Given either a price index or quantity index, the other function can be defined implicitly by Equation (6).

Implicit Tornqvist bilateral-aggregate output-price and input-price chain indices for the U.S. tropical tuna purse-seine fleet, along with the resource-abundance adjusted total-factor productivity index, are presented in Table 3 and in Figure 1. Increases in total-factor productivity or output prices, or both, improve the fleet's economic performance, while increases in input prices worsen the fleet's economic performance.

Taken together, the changes in total-factor productivity, aggregate input-price, and aggregate output-price indices shown in Figure 1 and Table 3 indicate that the 1981–85 period was highly unstable with regard to the fleet's economic performance. Herrick and Koplin (1986, 1987) point out that this was a time of massive restructuring in the U.S. tuna industry, during which the U.S. fleet began a significant shift of its operations from the eastern to the western Pacific

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[10] These period-to-period changes in total-factor productivity, i.e., productivity growth, were computed following footnote 6. Next, the exponent is taken of each value in column (5) of Table 1, giving $TFP_{t,t-1}$. The Tornqvist bilateral-chain index is then formed following Equation (4), to give the first column of Table 3. Note that the value 1.000 for 1981 is the exponent of zero, where zero refers to the zero change for the first period.

Ocean, and the U.S. canned tuna market was inundated by imports. These events undoubtedly contributed to the unstable pattern of productivity growth, and would have introduced additional, unmeasurable disturbance into the system which we are unable to disentangle from the productivity residual in the growth-accounting framework.[11]

Concluding remarks

We have shown how the nonparametric growth-accounting framework can be modified to measure the growth in total-factor productivity or technical progress of fishing fleets. This framework can provide useful information for tracking and analyzing economic growth and its causal factors in a fishing industry, particularly where short time-series of aggregate data are all that is available. Our approach can be readily implemented in fishing industries in both developed and developing countries, even by non-economist fishery analysts. Unique to our approach is the treatment of the fishery resource, not as a conventional input, but as a technological constraint on production. Our empirical analysis of total-factor productivity growth in the U.S. tropical tuna fleet demonstrates that disentangling the productivity residual from changes in resource abundance provides markedly different results.

We consider capital the most important component of aggregate input because it is represented by the basic unit of production, the fishing vessel. The capital stock—the fishing fleet—determines capacity output in both an economic and engineering sense. Theoretically, it is the flow of services from the capital stock that should serve as the capital input when measuring total-factor productivity. In practice, however, one may not have measures of the flow of capital services, in which case proper specification of the capital input, and accounting for temporary equilibrium effects such as variations in the degree of capacity utilization, becomes extremely important.

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Citations

Bell, F., and R. Kinoshita
1973 Productivity gains in U.S. fisheries. Fish. Bull., U.S. 71:911–919.

Berndt, E., and M.A. Fuss
1986 Productivity measurement with adjustments for variations in capacity utilization and other forms of temporary equilibrium. J. Econom. 33:7–29.

Clark, C.
1976 Mathematical bioeconomics. Wiley, NY..

Cowing, T., J. Small, and R. Stevenson
1981 Comparative measures of total factor productivity in the regulated sector: The electric utility industry. *In* Cowing, T., and R. Stevenson (eds.), Productivity measurement in regulated industries, p. 162–177. Acad. Press, NY.

Dasgupta, P., and G. Heal
1979 Economic theory and exhaustible resources. Cambridge Univ. Press, Cambridge.

Davis, L.E., R.E. Gallman, and T.D. Hutchins
1987 Technology, productivity and profits: British-American whaling competition in the North Atlantic, 1816–1842. Oxford Econ. Papers 39:738–759.

Denny, M., M. Fuss, and L. Waverman
1981 The measurement and interpretation of total factor productivity in regulated industries, with an application to Canadian telecommunications. *In* Cowing, T., and R. Stevenson (eds.), Productivity measurement in regulated industries, p. 179–212. Acad. Press, NY.

Duncan, I.
n.d. New Zealand's inshore fishery: A summary of economic conclusions and management options. N.Z. Fishing Industry Board, Wellington, mimeo.

Fisher, I.
1922 The making of index numbers. Houghton Mifflin, Boston.

Gordon, H.S.
1954 The economic theory of a common property resource: The fishery. J. Political Econ. 62:124–142.

Herrick, S., Jr., and S. Koplin
1986 U.S. tuna trade summary, 1984. Mar. Fish. Rev. 48(3): 28–37.
1987 U.S. tuna trade summary, 1985. Mar. Fish. Rev. 49(3): 73–84.

Hulten, C.R.
1974 Divisia index numbers. Econom. 41:1017–1025.
1986 Productivity change, capacity utilization, and the sources of efficiency growth. J. Econom. 33:31–50.

International Trade Commission (ITC)
1986 Competitive conditions in the U.S. Tuna industry: Report to the President on investigation no. 332224 under section 332 of the Tariff Act of 1930. U.S. Int. Trade Comm., Wash., DC 20436, 320 p.

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[11] Because our biomass adjustment is based only on changes in yellowfin tuna resource abundance in the CYRA, the variation in total-factor productivity should become more pronounced as the fleet moved from the eastern to the western Pacific Ocean during the 1981–85 period. Furthermore, there were likely to have been some initial technical inefficiencies as the fleet began fishing in the relatively unfamiliar western Pacific.

New investment and industry restructurings can have very real detrimental effects upon the time-path of productivity growth. Therefore, we would expect to see unstable productivity growth as firms adapt over time to changing industrial conditions. Under such circumstances, the assumptions underlying our model—constant-returns-to-scale, disembodied Hick's-neutral technical change conditions, and technical efficiency—may not fully apply. Nonetheless, these are limitations of virtually any application using the growth-accounting framework.

Kirkley, J.
1984 Productivity in fisheries. Discussion pap., Woods Hole Lab., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543, 20 p.

McFadden, D.
1978 Cost, revenue, and profit functions. *In* Fuss, M., and D. McFadden (eds.), Production economics: A dual approach to theory and applications, vol. 1, p. 3–109. North-Holland Press, Amsterdam.

Nelson, R.
1981 Research on productivity growth and productivity differences: Dead ends and new departures. J. Econ. Lit. 19:1029–1064.

Norton, V., M. Miller, and E. Kinney
1985 Indexing the economic health of the U.S. fishing industry's harvesting sector. NOAA Tech. Memo. NMFS-F/NEC-40, Northeast Fish. Cent., Natl. Mar. Fish. Serv., Woods Hole, MA 02543, 42 p.

Schaefer, M.B.
1957 A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull. 6, Inter-Am. Trop. Tuna Comm., La Jolla, CA 92038, p. 247–285.

Scott, A.
1954 The fishery: The objectives of sole ownership. J. Political Econ. 63:116–124.

Solow, R.
1957 Technical change and the aggregate production function. Rev. Econ. Stat. 39:312–320.

Squires, D.
1988 Index numbers and productivity measurement in multispecies fisheries: An application to the Pacific coast trawl fleet. NOAA Tech. Rep. NMFS 67, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 34 p.

Squires D., and S. Herrick, Jr.
1988 Productivity measurement in common property resource industries: An application to the Pacific coast trawl fishery. Mimeo rep., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 34 p.

Tornqvist, M.A.
1936 The Bank of Finland's consumption price index. Monthly Bull. Bank of Finland 10:27–34.

Appendix

The growth-accounting framework is developed by differentiating Equation (1) with respect to time t:

$$\frac{dY(t)}{dt} = \sum_{i=1}^{N+1} \frac{\delta F}{\delta X_i(t)} \cdot \frac{dX_i(t)}{dt} + \frac{\delta F}{\delta A(t)} \cdot \frac{dA(t)}{dt} + \frac{\delta F}{\delta B(t)} \cdot \frac{dB(t)}{dt}, \qquad \text{(A.1)}$$

where $dY(t)/dt$ represents the growth rate of output (i.e., extraction rate) due to technical progress. Putting the left side of Equation (A.1) into percentage terms (and suppressing the notation for each time period t) gives:

$$\frac{dY}{dt}\frac{1}{Y} = \frac{1}{F} \left[\sum_{i=1}^{N+1} \frac{\delta F}{\delta X_i}\frac{dX_i}{dt} + \frac{\delta F}{\delta A}\frac{dA}{dt} + \frac{\delta F}{\delta B}\frac{dB}{dt} \right]. \qquad \text{(A.2)}$$

To obtain proportionate growth rates for all variables, substitute $[dY/dt]\,[1/Y] = \dot{Y}/Y$, $[dX_i/dt]\,[1/X_i] = \dot{X}_i/X_i$, $[dA/dt]\,[1/A] = \dot{A}/A$, and $[dB/dt]\,[1/B] = B/B$ into Equation (A.2) to give:

$$\frac{\dot{Y}}{Y} = \sum_{i=1}^{N+1} \left[\frac{\delta F}{\delta X_i}\frac{X_i}{F} \right] \frac{\dot{X}_i}{X_i} + \left[\frac{\delta F}{\delta A}\frac{A}{F} \right] \frac{\dot{A}}{A} + \left[\frac{\delta F}{\delta B}\frac{B}{F} \right] \frac{\dot{B}}{B}. \qquad \text{(A.3)}$$

In equation (A.3), by convention (Denny et al. 1981, Solow 1957) the term $[\delta F/\delta A]\,[A/F]$ is the proportional shift in the production function with time and is set equal to unity. Thus a 1% increase in the index of technical progress increases the flow rate of output by 1%. This shifting of the production function through time is called technical change or the time rate of growth of technical progress. The term $[\delta F/\delta B]\,[B/F]$ is set to unity because it is a technology-shift parameter for a Schaefer (1957)-type production technology in which catch rates are proportional to resource abundance for any given vector of inputs.[12]

Define $E_i = [\delta F/\delta X_i]\ [X_i/F]$. This is the output elasticity of input X_i, representing the proportional change in output flow for a given change in X_i within some level of resource stock abundance and state of technological progress. Substituting the output elasticity expression into (A.3) gives the long-run rate of output growth as:

$$\frac{\dot{Y}}{Y} = \sum_{i=1}^{N+1} E_i \frac{\dot{X}_i}{X_i} + \frac{\dot{A}}{A} + \frac{\dot{B}}{B}, \qquad \text{(A.4)}$$

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[12] This corresponds to the production function specified by Schaefer (1957), $Y = F(E,B) = qEB$, where q denotes the catchability coefficient and E represents effort or an aggregate input index so that $E = g(X_i, \ldots, X_{N+1})$, where g is a linearly homogeneous aggregator function and the $N+1$ X_i are the inputs. Thus, $\delta Y/\delta B = 1$. We are grateful to Jim Kirkley who pointed this out to us. Moreover, the Schaefer production function implicitly assumes constant-returns-to-scale in inputs, because $\delta Y/\delta E = 1$, so that a proportionate increase in E generates an equal proportionate increase in Y. In addition, changes in the resource stock affect the production function in a Hick's-neutral manner, similar to technical progress.

or after rearranging:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} E_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \qquad \text{(A.5)}$$

where the dots over the variables represent time derivatives.

Equation (A.5) is the fundamental equation of growth accounting in its continuous time form. Thus full, long-run equilibrium total-factor productivity growth, $\dot{A}/A$, identified with technical progress, is a residual after the sources of output growth have been allocated among intertemporal changes in inputs and resource abundance for a constant-returns-to-scale production technology.

Equation (A.5) allocates the growth rate of $Y(t)$ among $A(t)$, $X(t)$, and $B(t)$ as required, but because the E_i are not observable, two additional steps are required for empirical analysis. Assuming that all inputs are paid the value of their marginal product, then $\delta F/\delta X_i(t) = P_i(t)/P(t)$, where $P(t)$ and $P_i(t)$ are the full equilibrium prices of output and inputs, respectively. This implies that: $S_i(t) = E_i(t) = P_i(t)X_i(t)/P(t)Y(t)$, where $S_i(t)$ is the income or cost share of input X_i. Under constant returns to scale, total costs equal total revenue; i.e., $\Sigma_i P_i(t)X_i(t) = P(t)Y(t)$, and $\Sigma_i S_i(t) = 1$.

The final step is to substitute $E_i(t) = S_i(t)$ into equation (A.5), which gives an equation in which all variables are measurable except $\dot{A}/A$, which is calculated as a residual:

$$\frac{\dot{A}}{A} = \frac{\dot{Y}}{Y} - \sum_{i=1}^{N+1} S_i \frac{\dot{X}_i}{X_i} - \frac{\dot{B}}{B}, \qquad \text{(A.6)}$$

where the notation for time-period t is again suppressed and $\Sigma_i S_i(\dot{X}_i/X_i)$ represents aggregate input growth. Productivity growth equals the rate of change of output flow minus a share-weighted index of rates of change of inputs minus the rate of change of the resource stock. The index of productivity growth in Equation (A.6) is also called a Divisia index (Hulten 1974).

Abstract.–Optimal harvesting policies were developed for a model of the Washington-Oregon-California trawl fisheries for bocaccio *Sebastes paucispinus*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*. In the simulated management system, the annual quota for each species was based on an intended fishing mortality rate (F) and an estimate of stock biomass. Traditional constant F policies were compared with variable F policies in which F was a linear function of either stock biomass (single-species) or the combined biomass of all other species (multispecies). Variable F policies were ineffective for increasing total harvest of all species combined, when compared with constant F policies. However, both single-species and multispecies variable F policies were found to reduce the variance for total harvest substantially with no significant loss in yield. The reduction in variance was roughly equal to the reduction that would be achieved by lowering the coefficient of variation (CV) for biomass estimates from 50% to 25% or from 25% to 0%. The reduction in variance generally was greater for the multispecies than for the single-species variable F policy. Compared with the case where CV = 0%, average total yield was reduced slightly for both constant F and variable F policies when CVs for biomass estimates were greater than 0%.

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Multispecies Harvesting Policies for Washington-Oregon-California Rockfish Trawl Fisheries

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In the Washington-Oregon-California (WOC) trawl fisheries for rockfish (*Sebastes* spp.), the landings are comprised of many species, including bocaccio *S. paucispinus*, chilipepper *S. goodei*, Pacific ocean perch *S. alutus*, canary rockfish *S. pinninger*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus* (PFMC 1982). There is little evidence of substantial biological interaction among the adults of these species. Technological interactions (Pope 1979) are significant in the shelf rockfish fishery (Pikitch 1987), which accounts for most of the landings of bocaccio, chilipepper, and canary and yellowtail rockfish. Fishermen have some control over the species composition of the catch in this fishery by varying the areas or depths fished. The other significant rockfish fishery is the midwater trawl fishery for widow rockfish. Catches of other rockfish species are negligible in that fishery.

Most currently marketed *Sebastes* species have similar or equal value to fishermen; consequently, fishermen are more concerned about the aggregate yield than about the species composition of the catch. Thus, it seems reasonable to ask whether efforts to vary the annual proportions harvested for these species would result in benefits to the resource or to the fishing industry. For example, reducing the variability of annual quotas has been an important concern for the west coast fishing industry. The objective of this study was to evaluate multispecies harvesting policies for the WOC trawl fisheries for rockfish to determine whether total yield (all species combined) can be increased or the variance for total yield can be reduced. Specifically, I compared the performance of policies obtained using (1) risk-neutral and risk-averse objective functions, (2) constant and variable fishing mortality rates (F), and (3) abundance estimates for a single species or multiple species.

Except for widow rockfish, relatively little is known about the population dynamics of these stocks. For that reason, this study should be viewed as an exploratory analysis of alternative harvesting policies, and not as a basis for regulatory changes by the Pacific Fishery Management Council. It may be worthwhile to develop similar harvesting policies for Council review once we have adequate life-history information about the commercially important groundfish stocks. The harvesting policies examined in this study should be useful in other cases where fishermen derive income from several species and have some control over the species composition of the catch.

Methods

This section provides an overview of the model structure, harvesting policies, and life-history data. A detailed description of methods is provided elsewhere (Hightower 1990).

I developed optimal harvesting policies for two-, three-, and five-species models in order to evaluate changes in policy performance as additional species were included. The selected species (bocaccio, chilipepper, widow rockfish, splitnose rockfish *S. diploproa*, and shortbelly rockfish *S. jordani*) all occur off California, support or could support significant commercial fisheries, and have a wide range of life-history types. I used bocaccio and chilipepper for the two-species model because they were estimated to have similar biomass levels. I included widow rockfish for the three-species model because it was estimated to have about twice the maximum sustainable yield level of biomass of bocaccio and chilipepper. For the five-species model, shortbelly and splitnose rockfish were added as examples of relatively short- and long-lived rockfish species, respectively. Shortbelly rockfish biomass also is substantially higher than that of the other four species.

Model structure

I used Schnute's (1985) generalization (eq. 2.7) of Deriso's (1980) delay-difference model to represent the dynamics of each stock:

$$B_t = (1+\rho)S_{t-1}B_{t-1} - \rho S_{t-1}S_{t-2}B_{t-2} + R_t - \rho(v/V)S_{t-1}R_{t-1} \qquad (1)$$

where B_t was the fishable population biomass at the beginning of year t; S_t was the survival rate in year t; ρ, v, and V were parameters for the growth curve; and R_t was the recruitment biomass at the beginning of year t. Growth parameters ρ, v, and V were estimated by fitting the following curve relating mean weight at age a (w_a) to age:

$$w_a = v + (V-v)(1-\rho^{1+a-k})/(1-\rho) \qquad (2)$$

where V and v were parameters representing mean weight at the age of recruitment (age k) and at age k−1, respectively, and ρ was a parameter describing the growth rate (Schnute 1985, eq. 1.14). Following Kimura et al. (1984), I assumed that B_0 (needed to calculate B_2) equaled the starting biomass level B_1.

Recruitment was calculated from a Beverton-Holt stock-recruitment curve (Kimura 1988):

$$R_{t+k} = R_\infty(B_t/B_\infty)/(1-A(1-B_t/B_\infty))\exp(z_t) \qquad (3)$$

where R_∞ was the virgin recruitment level associated with virgin stock biomass B_∞, A was the level of density-dependence assumed in the stock-recruitment relationship, and $\exp(z_t)$ was the lognormal error term used to introduce random variability in recruitment. Estimates of A were not available for any of the stocks used in this study. To introduce a degree of density-dependence into the model, I assumed arbitrarily that recruitment decreased by 10% when spawning stock decreased by 50%. That assumption has been used in earlier stock-assessment studies (Lenarz 1984, Henry 1986, Methot and Hightower 1988, Tagart 1988) to obtain harvest recommendations assumed to be conservative when information on the stock-recruitment relationship was unavailable. The normal random variate z_t was assumed to have mean 0 and variance σ^2. I assumed that $R_1 \ldots R_k$ were produced by a stock equal in size to B_1 because the actual B values producing those year-classes were not known.

Harvesting policies

In the harvesting policies used in this study, the annual fishing mortality rate for species j in year t ($F_j[t]$) was either a constant

$$F_j[t] = b_{j,0} \qquad \text{(constant F)}, \qquad (4)$$

a function of stock biomass

$$F_j[t] = b_{j,0} + b_{j,1}\, B_j[t] / B_{\infty,j} \qquad \text{(variable F)}, \qquad (5)$$

or a function of the combined biomass of all other stocks

$$F_j[t] = b_{j,0} + b_{j,1} \sum_{i\neq j} B_i[t] \Big/ \sum_{i\neq j} B_{\infty,i}, \qquad \text{(multispp. var. F)} \qquad (6)$$

Policies (5) and (6) were similar in form to a linear model Hilborn (1985) used to calculate catch as a function of stock biomass. Biomass estimates were scaled by virgin biomass so that the policy parameters were relatively independent of absolute biomass levels. Estimates of the policy parameters ($b_{j,0}$, $b_{j,1}$; $j=1,\ldots,s$ species in model) were obtained using stochastic approximation (Ruppert et al. 1984).

Objective functions

As in earlier optimization studies (Ruppert et al. 1984, Hilborn 1985), I obtained policies for maximizing total catch

$$\max \sum_t C[t], \text{ where } C[t] = \sum_j C_j[t] \qquad \text{(maxh objective function)}$$

and the natural logarithm of total catch

$$\max \sum_t \log(C[t]) \qquad \text{(logh objective function).}$$

For most of the WOC trawl fisheries, the goal of the Pacific Fishery Management Council is to maximize long-term average yield by maintaining F at a specified level. Thus the maxh objective function corresponds to the current approach to management. Relative to maxh policies, logh policies tend to provide less variable catches so they may be more appropriate in fisheries where price is sensitive to volume, the fishery provides a substantial fraction of a fisherman's annual income, or stability of volume is critical for marketing reasons (Deriso 1985). Mendelssohn (1982) and Ruppert et al. (1985) used maxh and logh policies to represent extremes along a risk continuum, in that maxh policies are risk-neutral (marginal utility does not change with increasing catch) and logh policies are risk-averse (marginal utility decreases with increasing catch).

I also evaluated a third more conservative objective function for maximizing an exponential function of total catch:

$$\max \sum_t (1 - \exp(-C[t]/\delta)) \qquad \text{(negx objective function)}$$

where δ was a scaling factor (Raiffa 1968). At small values of δ (relative to C[t]), the marginal utility of additional units of catch decreases rapidly. If δ is large, utility increases linearly with increasing catch. In order to obtain highly risk-averse policies, I used $\delta = 5$ for C[t] values of about 5 (2-species case) to 30 (5-species case). Using this δ value, negx policies were even more conservative than logh policies (Fig. 1). Of course, other objective functions (and harvesting policies) could be chosen that would provide greater reductions in the variance of catch. For example, Murawski and Idoine (1989) compared a series of constant-catch harvesting policies for Georges Bank haddock *Melanogrammus aeglefinus*. For a sufficiently low target catch (45% of the average catch under a constant $F = F_{0.1}$ policy), year-to-year variability in catch was zero. The logh and negx objective functions used in this study were intended to provide a compromise between maximizing catch and minimizing variability of catch.

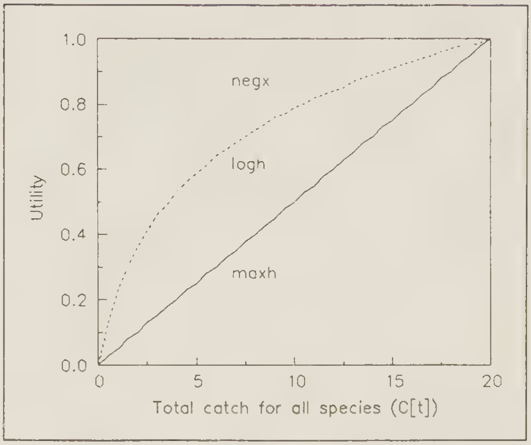

Figure 1

Alternative measures of the utility of the total rockfish catch in year t (C[t]), as determined by objective functions maxh:Utility(C[t]) = C[t], logh:Utility(C[t]) = $\log_e$(C[t]), and negx:Utility(C[t]) = 1 − exp(− C[t]/5). Utilities for each objective function were scaled to a maximum value of 1.

Planning horizon

The optimization studies were done using a 100-year planning horizon in order to obtain steady-state harvesting policies. In the two- and three-species cases, the bocaccio, chilipepper, and widow rockfish stocks declined to varying degrees at the start of the planning horizon but reached steady-state levels by about year 50 (Fig. 2). In the five-species case, sharp initial declines were noted for the unexploited splitnose and shortbelly rockfish stocks. Because of its long life-span and slow growth-rate, the splitnose rockfish stock continued to decline throughout the planning horizon. Based on a series of optimization runs, I found that the constant F for splitnose rockfish that maximized mean harvest decreased as the horizon length increased for policies up to 200 years in length. Planning horizons greater than 100 years were impractical, however, due to computing costs. Therefore, in order to obtain results that were not dependent on the length of the planning horizon, I obtained policies for the five-species model using a 75-year transient phase within a 100-year horizon (Law and Kelton 1982). Using this approach, the objective function was based only on harvests in years 75–100. Steady-state biomass levels were reached within 100 years for all species except possibly splitnose rockfish; thus, declines in stock size at the start of the planning horizon were due only to high initial biomass levels (Fig. 3).

Errors in biomass estimates

Most of the harvesting policies evaluated in this study required biomass estimates for one or more species in order to calculate the policy Fs used to determine the annual quotas. To evaluate the practicality of these policies, I introduced a random error term so that the harvesting policy and resultant catch quota in year t were based on simulated estimates $B'_1[t]..B'_s[t]$ of

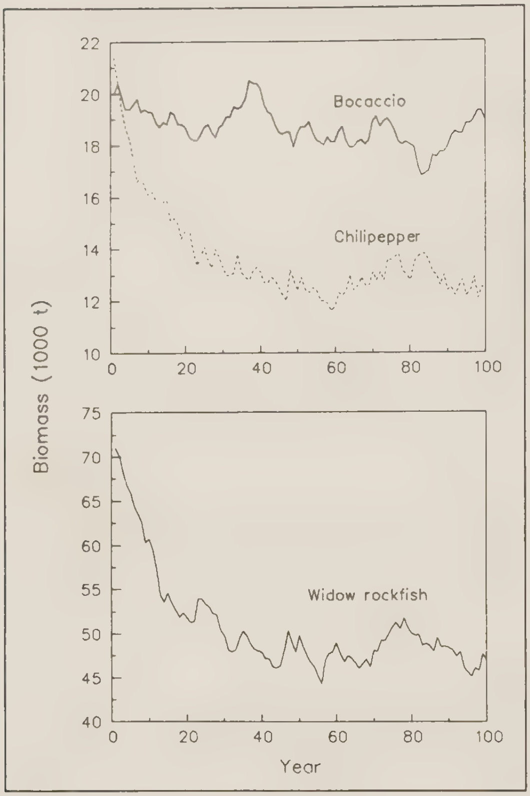

Figure 2

Mean rockfish biomass from 100 replicate 100-year simulation runs for the three-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0. Results for the two-species model with only bocaccio and chilipepper were similar and are not shown here.

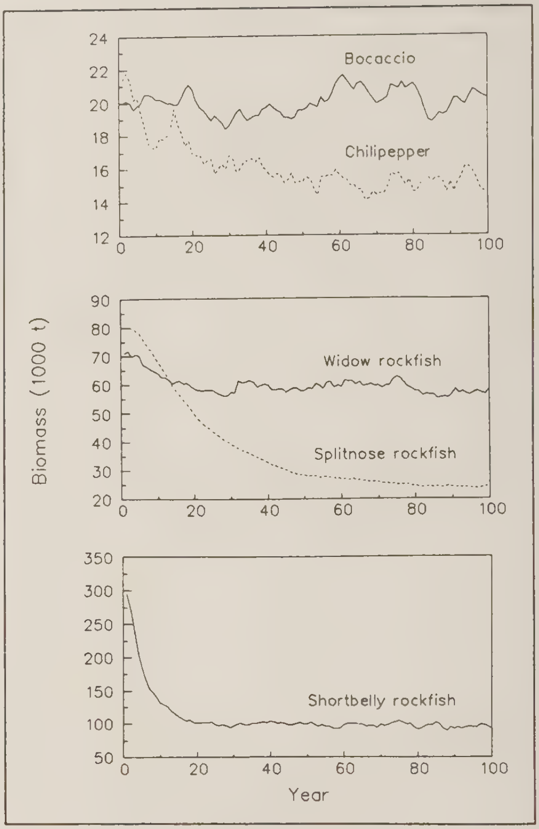

Figure 3

Mean rockfish biomass from 100 replicate 100-year simulation runs for the five-species model, using the constant fishing mortality rates that maximized harvest and assuming that the coefficient of variation for biomass estimates was 0.

the actual biomass levels $B_1[t]..B_s[t]$. Following an assumption made by Pope and Gray (1983) regarding data used in stock assessments, I assumed that errors in biomass estimates were lognormally distributed and independent over time. The coefficient of variation (CV) for biomass estimates was either 0, 25, or 50%, based on a review of the stock-assessment literature (Rivard 1981, Pope 1983, Pope and Gray 1983, Sen 1984, Weinberg et al. 1984, Methot 1986).

Because the WOC trawl fisheries for rockfish are regulated through catch quotas, F′ (the policy F based on estimates $B'_1[t]..B'_s[t]$) was used to calculate the annual quota $C_j[t]$ as $B'_j[t]F'_j[t](1 - \exp(-M_j - F'_j[t])/Z'_j[t]$. $B_{\infty,i}$ (the virgin biomass level used in the variable F policies) and M_j were assumed to be known without error. The actual F required to obtain $C_j[t]$ from $B_j[t]$ ($F_j[t]$) was either higher or lower than the intended F ($F'_j[t]$), depending on the direction and magnitude of errors in $B'_1[t]..B'_s[t]$.

Life-history information

The reliability of the parameter estimates (Table 1) varies, depending on the length and magnitude of the historical fishery for each species. A significant fishery for widow rockfish developed in 1979, with average 1980–85 landings of 17200 t (Hightower and Lenarz 1986). Fisheries for bocaccio and chilipepper have existed for decades; average 1980–85 landings were 3200 t for bocaccio and 1700 t for chilipepper (PFMC 1986). Preliminary stock assessments based on catch-at-age data have been completed for all three species. Land-

Table 1

Parameters used in delay-difference models for each rockfish species. Methods used to estimate the life-history parameters are described in detail by Hightower (1990).

	widow	bocaccio	chilipepper	splitnose	shortbelly
k	6	4	8	12	4
v (kg)	0.436	0.061	0.581	0.327	0.078
V (kg)	0.598	0.553	0.796	0.343	0.110
ρ	0.903	0.933	0.878	0.984	0.825
M	0.15	0.25	0.20	0.05	0.20
B_∞ (t)	180.0	60.0	47.7	80.0	295.0
B[1] (t)	71.0	20.0	21.4	80.0	295.0

Table 2

Fishing mortality rates of rockfish obtained for constant F policies maximizing harvest (maxh), log(harvest) (logh), or a negative exponential function of harvest (negx) for two-, three-, and five-species models.

		Fishing mortality rate				
Species	Objective function	bocaccio	chilipepper	widow	splitnose	shortbelly
Two	maxh	0.200	0.269	–	–	–
	logh	0.195	0.255	–	–	–
	negx	0.194	0.250	–	–	–
Three	maxh	0.201	0.264	0.181	–	–
	logh	0.196	0.254	0.174	–	–
	negx	0.191	0.242	0.163	–	–
Five	maxh	0.182	0.222	0.153	0.056	0.229
	logh	0.181	0.218	0.152	0.055	0.224
	negx	0.187	0.211	0.146	0.055	0.204

ings of splitnose and shortbelly rockfish have been negligible to date; consequently, parameter estimates for those species should be viewed as highly preliminary.

Results and discussion

Objective functions

Results were similar for constant F policies using different objective functions. Optimal constant Fs generally were comparable with M, although the F for chilipepper (M = 0.20) was higher than that for bocaccio (M = 0.25) (Table 2). That apparently was due to the higher age at first recruitment for chilipepper. (For bocaccio and chilipepper, the slight differences in constant Fs in the two- and three-species cases were due to random error.) Optimal Fs were lower for the five-species case than for the two- and three-species cases because harvests in years 1–74 were excluded from the five-species objective function. Policies obtained assuming a transient period may be unacceptable on socioeconomic grounds but can probably be viewed as a practical lower bound for F.

For each of the models, the differences in F, total yield, and variance for total yield showed a consistent trend: highest for maxh policies, intermediate for logh policies, and lowest for negx policies (Tables 2–5). Relative to the variance for maxh policies, logh constant F policies resulted in about a 2% reduction in total variance, whereas variances for the negx policies were 3 (2-species case) to 10% (5-species case) lower. These results illustrate that moderately lower variances can be achieved by using slightly lower Fs and accepting slightly lower total yields.

Constant vs. variable F policies

The variable F policies (5)–(6) for maximizing harvest did not increase total yield significantly compared to the constant F policies (Tables 3–5). Results from earlier studies suggest that the degree of increase due to a variable F policy may depend on the assumed life-history characteristics. For example, a 17% increase

Table 3

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 0%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chilipepper	widow	splitnose	shortbelly	total	bocaccio	chilipepper	widow	splitnose	shortbelly	total
Two	const F	maxh	3.02	2.96	—	—	—	5.98	0.97	1.46	—	—	—	2.87
		logh	3.02	2.96	—	—	—	5.98	0.96	1.42	—	—	—	2.81
		negx	3.02	2.95	—	—	—	5.97	0.95	1.40	—	—	—	2.78
	variable F	maxh	3.05	3.02	—	—	—	6.05	1.49	3.81	—	—	—	6.00
		logh	3.03	2.96	—	—	—	5.96	0.91	1.17	—	—	—	2.44
		negx	3.02	2.95	—	—	—	5.95	0.84	1.09	—	—	—	2.27
	multispp.	maxh	3.02	2.96	—	—	—	5.98	0.95	1.48	—	—	—	2.83
		logh	3.00	2.95	—	—	—	5.95	0.92	1.36	—	—	—	1.94
		negx	2.99	2.94	—	—	—	5.93	0.95	1.32	—	—	—	1.70
Three	const F	maxh	3.02	2.95	7.78	—	—	13.75	1.01	1.28	4.92	—	—	7.40
		logh	3.04	2.94	7.77	—	—	13.75	1.01	1.26	4.85	—	—	7.29
		negx	3.03	2.93	7.75	—	—	13.71	1.00	1.23	4.72	—	—	7.12
	variable F	maxh	3.06	3.01	7.92	—	—	13.93	1.47	3.08	14.12	—	—	18.55
		logh	3.05	2.97	7.82	—	—	13.78	1.18	1.34	4.86	—	—	7.59
		negx	3.03	2.93	7.70	—	—	13.61	0.93	1.04	3.72	—	—	5.75
	multispp.	maxh	3.03	2.94	7.77	—	—	13.74	1.01	1.28	4.96	—	—	7.74
		logh	3.02	2.94	7.75	—	—	13.70	1.02	1.26	4.68	—	—	5.60
		negx	2.98	2.91	7.70	—	—	13.60	1.06	1.20	4.36	—	—	4.08
Five	const F	maxh	3.04	2.85	7.82	1.97	19.92	35.59	1.13	0.74	5.90	0.08	69.56	78.05
		logh	3.05	2.86	7.84	1.94	19.93	35.48	1.13	0.73	5.86	0.08	67.97	76.42
		negx	3.05	2.85	7.82	1.94	19.58	35.09	1.14	0.72	5.73	0.08	61.90	70.19
	variable F	maxh	3.06	2.90	7.95	2.30	20.84	36.91	1.53	1.22	16.96	0.21	431.37	460.41
		logh	3.06	2.89	7.91	2.43	20.02	36.17	1.40	0.84	7.56	0.25	70.84	82.13
		negx	3.03	2.85	7.70	1.49	18.58	33.53	0.99	0.70	3.70	0.20	26.41	32.10
	multispp.	maxh	3.03	2.87	7.85	1.99	20.07	35.67	1.18	0.74	5.90	0.08	70.92	78.16
		logh	2.89	2.58	7.52	1.37	19.61	33.83	1.28	0.93	6.01	0.63	68.64	44.60
		negx	2.46	2.64	7.72	1.41	19.37	33.46	1.64	0.69	5.52	0.20	59.66	43.70

in yield was reported for Atlantic menhaden *Brevoortia tyrannus* (Ruppert et al. 1985), compared with only 1–2% for Pacific whiting *Merluccius productus* (Swartzman et al. 1983) and widow rockfish (Hightower and Lenarz 1989). Because, in this study, there was no apparent advantage in using variable F policies to maximize harvest, the remaining results and discussion focus on a comparison of the traditional constant F policy for maximizing harvest versus variable F policies (5) and (6) for the logh and negx objective functions.

Compared with a constant F policy, variable F policies (5) and (6) provided a substantial reduction in the variance of total yield with only a negligible loss in yield. (The reductions in variance would be slightly less if constant F and variable F policies for the same objective function were compared.) The reduction in variance did not appear to be particularly sensitive to the number of species included, their life-history characteristics, or the degree of correlation among species for recruitment perturbations (Hightower 1990). However, the level of density-dependence in the stock-recruitment relationship may affect the relative performance of different harvesting policies. In limited additional runs, I found that the difference between constant F and variable F policies generally decreased as the degree of density-dependence increased (i.e., as stock-recruitment parameter A decreased). When recruitment declined markedly with reductions in spawning stock, both types of harvesting policies were necessarily quite conservative.

The advantage of the variable F policies can be illustrated by examining a Pareto Frontier (Walters 1975), which shows the relationship between mean catch and its variance. I developed frontiers for the two-, three-, and five-species cases by simulating the fishery at 20, 40, 60, 80, and 100% of the constant F levels that maximized harvest (Fig. 4). When results for the variable F policies were compared to the constant F frontiers, it was clear that the reduction in variance was much greater than could be accounted for by the lower yield

Table 4

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 25%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chilipepper	widow	splitnose	shortbelly	total	bocaccio	chilipepper	widow	splitnose	shortbelly	total
Two	const F	maxh	3.01	2.95	—	—	—	5.97	1.66	2.05	—	—	—	4.10
		logh	3.01	2.95	—	—	—	5.96	1.65	2.01	—	—	—	4.04
		negx	3.01	2.95	—	—	—	5.96	1.64	2.00	—	—	—	4.02
	variable F	maxh	3.04	3.00	—	—	—	6.02	3.33	5.57	—	—	—	9.60
		logh	3.01	2.95	—	—	—	5.93	1.28	1.41	—	—	—	3.00
		negx	3.00	2.93	—	—	—	5.91	1.17	1.26	—	—	—	2.72
	multispp.	maxh	3.01	2.95	—	—	—	5.97	1.65	2.06	—	—	—	4.10
		logh	2.99	2.94	—	—	—	5.92	1.79	1.96	—	—	—	2.44
		negx	2.98	2.93	—	—	—	5.90	1.86	1.95	—	—	—	2.25
Three	const F	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.05	8.58	—	—	11.58
		logh	3.02	2.94	7.75	—	—	13.72	1.61	2.03	8.51	—	—	11.50
		negx	3.02	2.93	7.73	—	—	13.68	1.60	2.00	8.39	—	—	11.34
	variable F	maxh	3.03	2.99	7.84	—	—	13.80	6.48	4.66	11.25	—	—	22.37
		logh	3.04	2.95	7.74	—	—	13.67	1.58	1.78	6.09	—	—	9.01
		negx	3.01	2.92	7.65	—	—	13.53	1.16	1.48	5.16	—	—	7.47
	multispp.	maxh	3.03	2.94	7.76	—	—	13.72	1.61	2.04	8.56	—	—	12.17
		logh	3.01	2.93	7.73	—	—	13.67	1.83	2.15	8.73	—	—	7.97
		negx	2.93	2.88	7.72	—	—	13.53	2.33	2.36	8.39	—	—	6.01
Five	const F	maxh	3.04	2.86	7.84	1.97	20.00	35.56	1.64	1.26	7.06	0.19	108.60	120.11
		logh	3.04	2.86	7.82	1.97	19.92	35.46	1.63	1.25	7.03	0.19	105.84	117.31
		negx	3.03	2.83	7.80	1.91	19.54	34.96	1.62	1.22	6.95	0.18	96.32	107.63
	variable F	maxh	3.05	2.89	7.90	2.33	20.70	36.74	2.88	3.95	14.34	2.75	958.44	987.02
		logh	3.04	2.87	7.84	2.25	19.55	35.43	1.80	1.54	6.71	0.34	66.07	78.42
		negx	2.99	2.82	7.66	2.22	18.10	33.67	1.04	0.84	4.70	0.34	31.20	40.20
	multispp.	maxh	3.01	2.86	7.84	2.00	20.01	35.59	1.71	1.27	7.07	0.19	107.71	115.41
		logh	2.91	2.56	7.35	1.39	19.60	33.66	1.82	1.51	8.72	1.13	110.50	66.74
		negx	2.22	2.31	7.08	1.14	19.47	32.09	2.79	1.77	9.08	1.48	95.97	40.77

obtained. In some cases, the reduction was comparable to the reduction that would be achieved by lowering the CVs for biomass estimates from 50% to 25% or from 25% to 0%. The percent reduction typically increased as the CVs for biomass estimates increased, although the loss in mean yield also increased somewhat (Hightower 1990).

Single-species vs. multispecies policies

When single-species (5) and multispecies (6) policies were compared, the variance for total catch generally was lower for the multispecies policy, except for some cases for the five- species model or when biomass CVs were 50%. In those cases, the better performance of the single-species policy probably was due to the feedback mechanism it contained. For example, in the five-species models, the single-species policies for shortbelly and splitnose rockfish could adapt to the large changes in the size of those stocks. When the five-species model was rerun using five "stocks" having chilipepper life-history characteristics, the variance for total catch was lower for the multispecies policy.

For the single-species policy, the variance of total catch typically was reduced by stabilizing the catch of each individual species (Tables 3–5). For the multispecies policy, reductions in the variance for total catch were sometimes achieved by increasing the variance for some of the less abundant individual species (Tables 3–5). The reduction in variance obtained using policy (6) is consistent with Clark's (1984) prediction that a multispecies system could be managed to reduce the variance of total yield, relative to the variance of the individual yields.

For the multispecies policies, the optimal parameter estimates were relatively insensitive to the objective function and to the CV for biomass estimates (Hightower 1990). The slope parameter $b_{j,1}$ was less than zero for all cases; consequently, fishing pressure varied inversely with the abundance of the other species.

Table 5

Comparison of average rockfish catches and year-100 variances for constant F, single-species variable F, and multispecies harvesting policies. CVs for biomass estimates were assumed to be 50%.

			Mean yield						Var[100]					
Species	Harvesting policy	Objective function	bocaccio	chili-pepper	widow	split-nose	short-belly	total	bocaccio	chili-pepper	widow	split-nose	short-belly	total
Two	const F	maxh	3.00	2.94	–	–	–	5.93	3.40	3.63	–	–	–	7.39
		logh	3.00	2.93	–	–	–	5.93	3.38	3.59	–	–	–	7.33
		negx	2.99	2.93	–	–	–	5.92	3.38	3.58	–	–	–	7.31
	variable F	maxh	3.02	2.97	–	–	–	5.96	8.49	12.36	–	–	–	21.14
		logh	2.97	2.91	–	–	–	5.85	1.84	1.83	–	–	–	4.06
		negx	2.95	2.90	–	–	–	5.83	1.68	1.69	–	–	–	3.77
	multispp.	maxh	3.00	2.94	–	–	–	5.93	3.40	3.65	–	–	–	7.48
		logh	2.96	2.91	–	–	–	5.87	4.04	3.76	–	–	–	4.24
		negx	2.96	2.90	–	–	–	5.86	4.06	3.91	–	–	–	4.09
Three	const F	maxh	3.01	2.92	7.72	–	–	13.65	3.35	4.42	19.06	–	–	24.74
		logh	3.01	2.92	7.72	–	–	13.64	3.35	4.37	19.03	–	–	24.70
		negx	3.01	2.91	7.69	–	–	13.61	3.34	4.30	18.90	–	–	24.53
	variable F	maxh	3.02	2.94	7.78	–	–	13.70	11.44	6.07	33.98	–	–	48.11
		logh	3.00	2.92	7.66	–	–	13.53	2.17	2.64	10.35	–	–	14.49
		negx	2.97	2.88	7.58	–	–	13.37	1.66	2.02	9.47	–	–	12.76
	multispp.	maxh	3.01	2.92	7.72	–	–	13.65	3.43	4.42	18.91	–	–	24.88
		logh	2.97	2.89	7.69	–	–	13.55	4.58	5.09	20.90	–	–	15.79
		negx	2.91	2.84	7.68	–	–	13.43	6.01	5.34	20.42	–	–	13.29
Five	const F	maxh	3.02	2.84	7.80	1.96	19.84	35.32	3.15	3.87	15.26	0.47	192.76	219.04
		logh	3.02	2.84	7.78	1.96	19.73	35.18	3.14	3.85	15.21	0.47	188.46	214.56
		negx	3.02	2.82	7.72	1.95	19.38	34.75	3.16	3.80	14.96	0.47	177.72	203.35
	variable F	maxh	3.03	2.86	7.81	2.18	20.43	36.18	5.26	10.09	120.32	4.15	1356.71	1540.97
		logh	3.02	2.82	7.78	1.43	18.64	33.56	2.90	1.52	11.61	0.54	64.10	84.87
		negx	2.96	2.78	7.51	1.52	17.32	31.96	1.53	1.26	7.28	0.42	43.02	55.69
	multispp.	maxh	3.00	2.84	7.79	1.97	19.91	35.38	3.34	3.88	15.26	0.47	191.10	209.32
		logh	2.92	2.64	7.44	1.57	19.58	34.01	3.58	3.45	18.95	1.68	208.31	135.32
		negx	2.08	2.28	7.05	1.37	19.20	31.84	7.13	4.10	20.26	2.46	173.92	81.64

Particularly in the three- and five-species cases, it appeared that the optimal multispecies strategy was to maintain stable catches for the species accounting for the majority of total yield, such as shortbelly or widow rockfish. Catches of less-abundant species (e.g., bocaccio or splitnose rockfish) varied depending on the abundance of the dominant species. For example, in the five-species case, the annual catch of splitnose rockfish was 0 in 24–30 of 100 years for the logh policies.

Errors in biomass estimates

Constant F policies were essentially identical when different CVs for biomass estimates were used. This indicates that the current management approach for Pacific Coast groundfish is robust to random, non-autocorrelated errors in estimating biomass. One obvious impact in the simulated fishery of introducing errors in estimating biomass was that the variance for total catch increased substantially (Tables 3–5, Fig. 4). This increased variability was due to differences between the intended (F) and actual (F′) fishing mortality rate. Such errors are nonlinearly related to estimated stock size and can be substantial (Rivard 1981). Rivard (1981) argued for higher precision in estimates of stock size in order to reduce the biological risk of applying $F' \gg F$ or the economic loss if $F' \ll F$. In this study, the variation in F due to errors in estimating biomass was much greater than that caused by using the variable F policies. For example, when CV = 0%, Fs for chilipepper in the five-species case ranged from 0.00 to 0.24 when using the multispecies logh model. When CV = 25%, the actual Fs ranged from 0.06 to 0.61 when the intended policy was a constant F of 0.22. Actual Fs ranged from 0.00 to 0.63 when CV = 25% and a multispecies logh policy was used, which suggests that multispecies policies do not introduce substantial additional risk, relative to the risk introduced by estimating biomass with error.

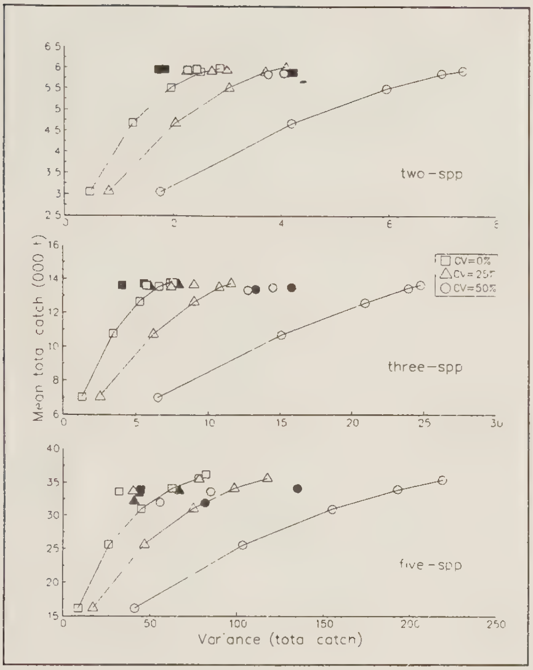

Figure 4

Relationship between mean total rockfish catch and the variance of total catch for the two- (bocaccio, chilipepper), three- (bocaccio, chilipepper, widow rockfish), and five-species (bocaccio, chilipepper, widow, splitnose, and shortbelly rockfish) models. Open symbols represent Pareto Frontiers derived by simulating the fishery at 20, 40, 60, 80, and 100% of the constant fishing mortality rate (F) that maximized harvest. Shaded and closed symbols represent the catch:variance relationship for the variable F and multispecies policies, respectively (equations 5–6). Simulation runs were made assuming a 0, 25, or 50% coefficient of variation for annual estimates of stock size.

Table 6

Average total rockfish catches and year-100 variances for constant F, variable F, multispecies, and three-parameter harvesting policies for the three-species model.

Biomass CVs	Policy	Objective function	Yield	Var[100]
0	(4)	maxh	13.75	7.40
	(5)	logh	13.78	7.59
	(6)	logh	13.70	5.60
	(7)	logh	13.77	6.39
	(5)	negx	13.61	5.75
	(6)	negx	13.60	4.08
	(7)	negx	13.60	4.09
25	(4)	maxh	13.72	11.58
	(5)	logh	13.67	9.01
	(6)	logh	13.67	7.97
	(7)	logh	13.63	6.99
	(5)	negx	13.53	7.47
	(6)	negx	13.53	6.01
	(7)	negx	13.51	5.40
50	(4)	maxh	13.70	24.74
	(5)	logh	13.53	14.49
	(6)	logh	13.55	15.79
	(7)	logh	13.50	11.39
	(5)	negx	13.37	12.76
	(6)	negx	13.43	13.29
	(7)	negx	13.33	8.21

Mean yield was only slightly lower at higher biomass CVs; the decrease was similar for constant F and variable F policies (Tables 3–5). Thus, in this model at least, there was no apparent disadvantage in using the more complex policies, even when biomass was estimated imprecisely. This was an interesting result because, although all policies used biomass estimates to calculate catch, the variable F policies also use the estimates to calculate Fs.

When biomass CVs were 50%, the variance for total catch was in all cases lower for the single-species (5) than for the multispecies policy (6). Apparently it was important to readjust continuously for the changes in stock size due to previous errors in estimating biomass. Based on limited additional runs using the three-species model, it appears that further gains in stability of total catch could be achieved by using a three-parameter harvesting policy (Table 6):

$$F_j[t] = b_{j,0} + b_{j,1} B_j[t] / B_{\infty,j} + b_{j,2} \sum_{i\neq j} B_i[t] / \sum_{i\neq j} B_{\infty,i}. \qquad (7)$$

The primary disadvantage of this policy is the computational expense required to obtain the policy parameter estimates.

Model limitations

One of the primary assumptions underlying this model is that trawlers can, on an annual basis, control the relative proportions of the individual rockfish species in the catch. That appears to be a reasonable assumption for widow rockfish, which are caught primarily in a directed midwater trawl fishery. Catches of other rockfish species should be low in a midwater trawl fishery for shortbelly rockfish (Lenarz 1980), and the Pacific Fishery Management Council is unlikely to permit a bottomtrawl fishery for that species. Peak abundance of splitnose rockfish is in deeper water than for the other species used in this model; however, some catches (particularly in the 100–149 fm depth interval) would likely contain bocaccio and chilipepper as well (Gunderson and Sample 1980). The greatest degree of overlap would be for bocaccio and chilipepper. Bocaccio occur over a greater latitudinal range than chilipepper, but in the area off California where both species are abundant, it could be difficult to maintain markedly different catch levels for the two species. An improved version of this model would incorporate probabilities for different levels of bycatch, so that the optimal policies would be constrained by the degree of targeting that was feasible (Pope 1979).

Another important assumption is that the species included in the objective function are interchangeable in the marketplace. That is a valid assumption for the commerically important *Sebastes* species, including widow rockfish, bocaccio, and chilipepper. However, demand for splitnose rockfish has been low because of its small size and low fillet yield (Lenarz 1986). A low price would be expected for shortbelly rockfish because they are small in size and must be processed rapidly (Lenarz 1986). Lenarz (1986) suggested that better marketing approaches will be needed before significant quantities of either splitnose or shortbelly rockfish can be harvested. For the model used in this study, differences in price among species could be accommodated easily and the objective function could be modified to maximize some function of income. It would also be of practical importance to determine whether all vessels participating in these fisheries caught all the species used in the objective function. Policies that result in variable catches of the species used in the model would be less appropriate if some fishermen did not catch or were unable to market some of the species.

The objective function could also be modified to include costs of fishing (see, for example, Pikitch 1987). However, the current practice of the Pacific Fishery Management Council is to manage for maximum sustainable yield; costs of fishing are not considered. Stock assessments are restricted to estimation of Acceptable Biological Catch (ABC), and the Council considers some socioeconomic factors when determining "Optimum Yield" from the ABC.

A limitation of this study was the assumption that model parameters M, B_∞, and A were known. Those parameters strongly affect equilibrium yields; consequently, when they are not well estimated, the passive policies used in this study might be outperformed by an adaptive probing strategy (Walters 1986). Under such a strategy, short-term fluctuations in fishing mortality and yield would be accepted in order to better estimate the productivity of the stock and improve long-term management.

Another potential limitation of the model used in this study was the assumption that errors in estimating biomass were not autocorrelated. That assumption may be valid when estimates are based on methods such as a swept-area trawl survey, although the fishery manager would be expected to balance any single estimate of stock size against observations from prior years. Autocorrelated errors would be likely in cases where estimates were based on a time-series of catch data. Such errors would be expected to have more serious consequences than the independent errors assumed here. An approach for introducing autocorrelated errors might be to use CVs of the same magnitude as assumed here but to use a 2- or 3-year moving-average estimate of biomass to set quotas. Errors in estimating biomass might also be correlated among species; for example, swept-area trawl surveys may underestimate the biomass of several species.

A possible limitation of this model was the assumption that the reliability of assessment data was equivalant for all species. If differences in the reliability of estimates were substantial, it might be found that a reliable single-species policy would be preferable to a multispecies policy that incorporated unreliable information on additional species.

Summary

1 When constant F policies for different objective functions were compared, the optimal F, total yield, and variance for total yield decreased as the level of risk aversion increased.

2 Single-species and multispecies variable F policies for maximizing harvest did not increase total yield significantly compared with constant F policies.

3 Single-species and multispecies variable F policies for the logh and negx objective functions provided a substantial reduction in the variance of total yield, compared with a constant F policy for maximizing harvest.

4 For the logh and negx objective functions, the variance for total catch was lower for the multispecies than for the single-species variable F policies, except for some cases for a five-species model or when biomass CVs were 50%.

5 Constant F policies for maximizing harvest (the current management approach) were essentially identical for different levels of random, non-autocorrelated errors in estimating biomass. Mean yield was slightly lower at higher biomass CVs for both constant F and variable F policies.

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Citations

Clark, C.W.
1984 Strategies for multispecies management: Objectives and constraints. *In* May, R.M. (ed.), Exploitation of marine communities, p. 303–312. Springer-Verlag, Berlin.

Deriso, R.B.
1980 Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37:268–282.
1985 Risk adverse harvesting strategies. Lect. Notes Biomath. 61:65–73.

Gunderson, D.R., and T.M. Sample
1980 Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3-4): 2–16.

Henry, F.D. Jr.
1986 Status of the coastwide chilipepper (*Sebastes goodei*) fishery. *In* Status of the Pacific Coast groundfish fishery through 1986 and recommended acceptable biological catches for 1987, Appendix 5. Pac. Fish. Manage. Counc., Portland, OR.

Hightower, J.E.
1990 Biomass-based models and harvesting policies for Washington-Oregon-California rockfish stocks with correlated recruitment patterns. NOAA-TM-NMFS-SWFC-137, Tiburon Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tiburon, CA 94920, 39 p.

Hightower, J.E., and W.H. Lenarz
1986 Status of the widow rockfish fishery. *In* Status of the Pacific Coast groundfish fishery through 1986 and recommended acceptable biological catches for 1987, Appendix 4. Pac. Fish. Manage. Counc., Portland, OR.
1989 Optimal harvesting policies for the widow rockfish fishery. Am. Fish. Soc. Symp. 6:83–91.

Hilborn, R.
1985 A comparison of harvest policies for mixed stock fisheries. Lect. Notes Biomath. 61:75–87.

Kimura, D.K.
1988 Stock-recruitment curves as used in the stock-reduction analysis model. J. Cons. 44:253–258.

Kimura, D.K., J.W. Balsiger, and D.H. Ito
1984 Generalized stock reduction analysis. Can. J. Fish. Aquat. Sci. 41:1325–1333.

Law, A.M., and W.D. Kelton
1982 Simulation modeling and analysis. McGraw-Hill, NY, 400 p.

Lenarz, W.H.
1980 Shortbelly rockfish, *Sebastes jordani*: A large unfished resource in waters off California. Mar. Fish. Rev. 42(3-4): 34–40.
1984 Status of the widow rockfish fishery. *In* Status of the Pacific Coast groundfish fishery and recommendations for management in 1985, Appendix 4. Pac. Fish. Manage. Counc., Portland, OR.
1986 A history of California rockfish fisheries. *In* Proc. Int. Rockfish Symp., Anchorage, Alaska, Oct. 1986, p. 35–41. Lowell Wakefield Fish. Symp. Ser. 5, Alaska Sea Grant, Univ. Alaska, Fairbanks.

Mendelssohn, R.
1982 Discount factors and risk aversion in managing random fish populations. Can. J. Fish. Aquat. Sci. 39:1252–1257.

Methot, R.D.
1986 Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. Admin. Rep. LJ 86-29, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 85 p.

Methot, R., and J. Hightower
1988 Status of the Washington-Oregon-California sablefish stock in 1988. *In* Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989, Appendix B. Pac. Fish. Manage. Counc., Portland, OR.

Murawski, S.A., and J.S. Idoine
1989 Yield sustainability under constant-catch policy and stochastic recruitment. Trans. Am. Fish. Soc. 118:349–367.

Pikitch, E.K.
1987 Use of a mixed-species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):349–359.

PFMC (Pacific Fishery Management Council)
1982 Final fishery management plan and supplemental environmental impact statement for the Washington, Oregon, and California groundfish fishery. Pac. Fish. Manage. Counc., Portland, OR.
1986 Status of the Pacific Coast groundfish fishery through 1986 and recommended acceptable biological catches for 1987. Pac. Fish. Manage. Counc., Portland, OR.

Pope, J.
1979 Stock assessment in multispecies fisheries, with special reference to the trawl fishery in the Gulf of Thailand. Rep. SCS/DEV/79/19, FAO South China Sea Fish. Dev. Coord. Prog., Manila, Philippines, 106 p. [ISBN 92-852-1011-2].

Pope, J.G.
1983 Analogies to the status quo TACs: Their nature and variance. *In* Doubleday, W.G., and D. Rivard (eds.), Sampling commercial catches of marine fish and invertebrates, p. 99–113. Can. Spec. Publ. Fish. Aquat. Sci. 66.

Pope, J.G., and D. Gray
1983 An investigation of the relationship between the precision of assessment data and the precision of total allowable catches. *In* Doubleday, W.G., and D. Rivard (eds.), Sampling commercial catches of marine fish and invertebrates, p. 151–157. Can. Spec. Publ. Fish. Aquat. Sci. 66.

Raiffa, H.
1968 Decision analysis. Introductory lectures on choices under uncertainty. Addison-Wesley, Reading, MA, 309 p.

Rivard, D.
1981 Catch projections and their relation to sampling error of research surveys. *In* Doubleday, W.G., and D. Rivard (eds.), Bottom trawl surveys, p. 93–109. Can. Spec. Publ. Fish. Aquat. Sci. 58.

Ruppert, D., R.L. Reish, R.B. Deriso, and R.J. Carroll
1984 Optimization using stochastic approximation and Monte Carlo simulation (with application to harvesting of Atlantic menhaden). Biometrics 40:535–545.
1985 A stochastic population model for managing the Atlantic menhaden (*Brevoortia tyrannus*) fishery and assessing managerial risks. Can. J. Fish. Aquat. Sci. 42:1371–1379.

Schnute, J.
1985 A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42:414–429.

Sen, A.R.
1984 Sampling commercial rockfish landings in California. Tech. Memo. NOAA-TM-NMFS-SWFC-45, Tiburon Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., Tiburon, CA 94920, 95 p.

Swartzman, G.L., W.M. Getz, R.C. Francis, R.T. Haar, and K. Rose
1983 A management analysis of the Pacific whiting (*Merluccius productus*) fishery using an age-structured stochastic recruitment model. Can. J. Fish. Aquat. Sci. 40:524–539.

Tagart, J.V.
1988 Status of the yellowtail rockfish stocks in the International North Pacific Fishery Commission Vancouver and Columbia areas. *In* Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989, Appendix D. Pac. Fish. Manage. Counc., Portland, OR.

Walters, C.J.
1975 Optimal harvesting strategies for salmon in relation to environmental variability and uncertain production parameters. J. Fish. Res. Board Can. 32:1777–1784.

Walters, C.
1986 Adaptive management of renewable resources. Macmillian, NY, 374 p.

Weinberg, K.L., M.E. Wilkins, and T.A. Dark
1984 The 1983 Pacific west coast bottom trawl survey of groundfish resources: Estimates of distribution, abundance, age and length composition. Tech. Memo. NMFS-F/NWC-70, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 376 p.

BIOECONOMIC EVALUATION OF THE CULTURE/STOCKING CONCEPT FOR CALIFORNIA HALIBUT

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ABSTRACT

We describe development of a model used to evaluate the bioeconomics of culture for stocking of the California halibut, *Paralichthys californicus*. Results from this model provide guidance for future research and preliminary estimates of feasibility. The model mimics growth of a cohort in culture from postlarvae to release, then in the ocean from release to mortality from natural causes or the fishery. Costs of culture and the benefits of cultured fish to the fishery are calculated. The latter are given in terms of number of released fish caught, biomass caught per release, cost per fish caught, and net benefit per released fish. The cost of post-larval fish is shown to be a substantial part of culture costs and should be reduced if possible. We demonstrate a graphical method for determining the release time that minimizes cost per recruit. For current parameter values this value is about 300 d. Both culture costs and optimal release time are sensitive to costs of food and space. We graphically show the trade-off between high growth rate and high costs of culture feeds. The cost of producing a recruit depends on post-release survival rate, but is not as sensitive as expected because of a compensatory shift in optimal release age. Costs per released fish caught could be near $5/fish if natural growth rates could be achieved in culture and the culture period could be extended to 300 d.

INTRODUCTION

In 1984 the Ocean Resources Enhancement Program (OREHP) began research to develop the biological and physical means to culture and stock California halibut, *Paralichthys californicus*, for fisheries enhancement. In addition to the biological research on culture and early life history (Gadomski et al. 1990), development of the culture/stocking concept required concurrent economic evaluation. On the basis of past experience, we began this kind of evaluation in the early stages of this project even before all of the data necessary to establish economic feasibility had been obtained. Although the ultimate goal of our economic evaluation was to determine feasibility and optimal manage ment policy, the main purpose of our early evaluation was to guide research and planning.

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We developed the mathematical models necessary for economic evaluation and performed the economic analysis possible with currently available data. We did this by developing several computer programs based on these models and incorporating available data into them. We then provided these models to other OREHP researchers so that they could continue the economic evaluation as additional data became available. These models will enable them to continue to evaluate the culture/stocking concept as research progresses by refining estimates of parameter values in the models and conducting further analysis. For information about the programs themselves see Appendix B.

Although the ultimate general goal of the evaluation is to determine economic feasibility (or at least to project the total costs of culture and benefits of stocking), other specific goals have been important in the early stages of the project. The primary purposes of the initial model were: (1) to evaluate dynamic behavior (i.e. to get an idea of how the system "works"), (2) to establish which of the needed pieces of information were available and which were outstanding, (3) to evaluate sensitivity of net benefits to unknown or poorly known parameters, and (4) to obtain a rough idea of the costs of culture and stocking.

We first present the relevant background on California halibut. This is a review of what is known about the life history, existing fisheries, and culture of these and related species. We then describe the models used in the computer programs that were developed to evaluate culture and stocking of this species. These use parameter values from the background section. Finally we present results of analyses using these programs and discuss their economic implications.

FISHERY AND CULTURE BACKGROUND

Development of a model of the culture, stocking, and fishery systems requires a review of available information. In this section, we describe existing information on life history, the fisheries, and culture performance for the California halibut. Information available on culture performance is limited; hence, some parameters from other similar species that have been cultured are used.

Life History and Fisheries

The California halibut supports both commercial and sport fisheries in southern California (Figure 1). It is fished in California and in Mexico and has experienced well-documented declines in catch leading to concern about the health of the stocks. The U.S. commercial catch reached a peak of 4.7 million pounds in 1919 and declined to 0.26 million pounds in 1971. Since then there is some evidence of a recovery. It is not known whether this is a result of the more restrictive regulations or due to natural fluctuations in abundance or availability (Methot 1983). For a more complete historical perspective see Barsky (1990).

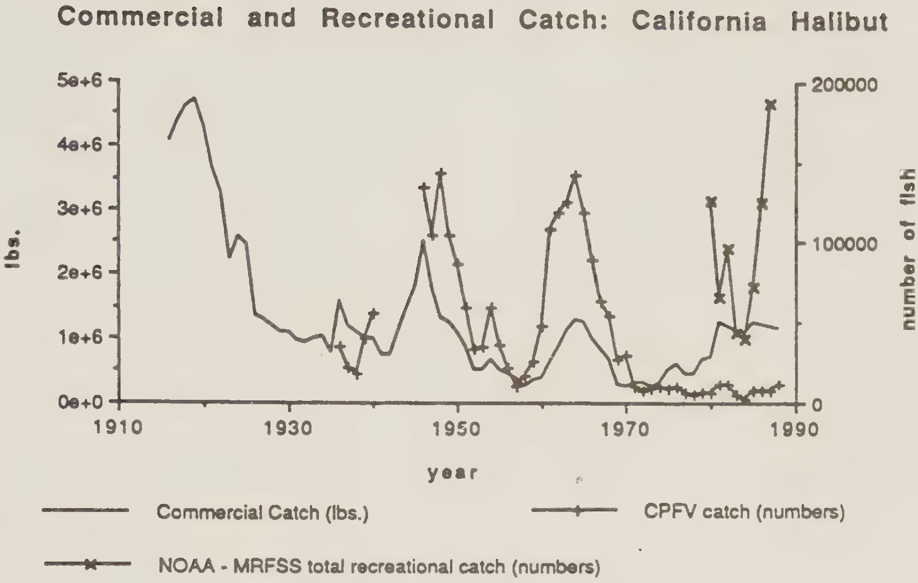

FIGURE 1. History of the California halibut fisheries. The solid line is the total harvest by commercial fishermen. The +'s are the harvest by commercial passenger fishing vessels. The X's are total harvests by sport fishermen.

The commercial fishery for California halibut has traditionally been primarily an otter trawl fishery but, in recent years, entangling nets have dominated the catch (Methot 1983). Since 1911 the use of otter trawls has been restricted in nearshore waters in southern California (Clark 1931). In 1971, regulations were enacted that allowed trawling within 3 mi of shore in the Santa Barbara Channel area. These same regulations established a minimum mesh size of 7.5 inches, a minimum size limit of 4 lb for commercially caught halibut, and season closures during the spawning season (Karpov 1981).

The sport fishery for California halibut is primarily a hook-and-line fishery that has operated from commercial passenger fishing vessels (CPFVs), man-made structures, shorelines, and private boats. The gear used is specialized and there is little incidental catch of other species. Since the late 1960s, CPFVs have not been able to profitably target on California halibut, and the proportion of the sport catch taken by private boats has increased (Methot 1983). Recently a sport fishery involving SCUBA gear and pole spear or spear gun has developed (C.A. Pattison, California Department of Fish and Game, pers. comm.). For a more complete historical description of the recreational fishery see Oliphant (1990) and Helvey and Witzig (1990).

In spite of the long history and the economic importance of this fishery, relatively little is known about the life history of California halibut. They spawn at depths of 6–20 m during the winter and spring, with the greatest frequency occurring from February to May. The larvae and postlarvae are pelagic (Frey 1971; Plummer et al. 1983; Lavenburg 1987). Young fish are common in embayments where they are believed to remain through the early juvenile phase, but it is not known whether the larvae settle in bays or migrate there after settlement (Plummer et al. 1983). The size distributions of fish caught in embayments and in shallow coastal waters suggest that juvenile halibut can reside in bays for a period of 2–3 years, reaching sizes there up to 30 cm standard length, but that most migrate to sea when they reach a length of about 20 cm (Frey 1971; Haaker 1975; Barry and Cailliet 1981; Kramer and Hunter 1987; Kramer 1990; Hammann and Ramirez-Gonzalez 1990). Males may begin to mature when they are in their second year, females 1 to 2 years later, and all fish are probably mature when they are 5 or 6 years old (Frey 1971). California halibut may live as long as 30 years and attain weights up to 23 kg (Frey 1971).

Growth patterns of the California halibut have have been reported in terms of length-at-age data and length-weight data. Length-at-age has been reported by Hulbrock (1974) for males ages 1 through 19 years and females ages 1 through 18 years, by Frey (1971) for females ages 1 through 12 years, and by Haaker (1975) for males and females ages 1 to 3 years. The three data sets appear to be consistent, so the data from Hulbrock were used to describe growth. We fit von Bertalanffy growth equations to the length-at-age data to obtain

$$L_t = 1130\,[1 - e^{(-0.1234\,t\,-\,0.1114)}] \qquad (1a)$$

for males and

$$L_t = 1440\,[1 - e^{(-0.118\,t\,-\,0.0852)}] \qquad (1b)$$

for females where L_t is total length in millimeters at age t years. The length-weight relationship for both sexes was determined by regression of Hulbrock's data to be

$$W_L = 7.811 \times 10^{-6}\,L^{3.048} \qquad (2)$$

where W_L is weight in grams at length L in millimeters. Reed and MacCall (1988) report parameter estimates similar to these.

The growth rate of juvenile fish during the first 2 years is less well known. A linear growth rate with intercept set at the initial post-larval size and the slope chosen so that size at 1 year corresponds to the von Bertalanffy growth equations for the California halibut population (analysis of data from Hulbrock 1974), would lead to a slope of 0.061 cm/d. However, the slope of the von Bertalanffy growth equation itself at 1 year is lower, 0.030 cm/d for males and 0.038 cm/d for females. Kramer and Hunter (1987, 1988) report a growth rate of 0.033 cm/d (10 mm/month from laboratory studies) and a size of 150 mm in bay/lagoon habitats at 9 months post settlement (0.039 cm/d). Growth of halibut in Todos Santos Bay fit a line with a slope of 9.51 cm/year and an intercept at 8.98 cm for ages 1 through 7 which indicates a growth rate of 0.051 cm/d during the first year and 0.026 cm/d in subsequent years (Hammann and Ramirez-Gonzalez 1990).

Adult mortality rates have not been directly estimated for California halibut. Reed and MacCall (1988) used a method based on the longevity of the species (cf. Hoenig 1983) to estimate the average annual instantaneous total mortality rate to be 0.15/year. This method is biased low depending on sample size (Hoenig 1983). In their analysis of the California halibut fishery, Reed and

MacCall (1988) used the values 0.1 and 0.2/year. The natural mortality rate for Pacific halibut, *Hippoglossus stenolepis*, off the coasts of Washington, British Columbia, and Alaska has been reported as 0.31/year, but this estimate may be biased upward because of loss of tags from fish used in these studies (Myhre 1967). The Pacific halibut used to estimate mortality rates were larger than the average size of the California halibut and so would be expected to have lower natural mortality rates (if mortality were due to predation). However, because of the potential bias in the estimate of mortality for Pacific halibut, 0.3/year is a reasonable upper limit for the natural mortality rate of adult California halibut. This value is consistent with values for similar species (Pauly 1979).

Mortality rates of juvenile halibut differ from those of adults but are similarly poorly known. Annual instantaneous mortality rates for a similar species, the speckled sanddab, *Citharichthys stigmaeus*, were estimated by Ford (1965). He estimated mortality rates both from the rate of decrease in density and directly from the age structure in 1962 and 1963. Because his age-structured estimates assume that recruitment has been constant, we have used only the estimates from the rate of decrease in density. The averages of the annual instantaneous mortality rates corresponding to the monthly percent survival reported by Ford are 2.286, 0.624, and 1.080/year for fish of age 0, 1, and 2; respectively. All three age classes of sanddabs are smaller than 1-year-old California halibut, thus the halibut would be expected to have lower mortality rates at age. In view of the paucity of mortality rate estimates for California halibut, we use a range of natural mortality rates in our economic evaluation.

Culture Performance

The information required to develop a model of the culture system comes from several sources. Biological information on culture of this species is relatively scarce, hence we have had to rely in part on information from other cultured species. Information on the components of the physical plant and their costs are also occasionally borrowed from other culture schemes.

The biological information needed for aquaculture is a description of how the organism responds to the environment provided in the culture system. In particular this would be growth, survival, food and oxygen consumption, waste production, and subjective criteria such as fitness for stocking or condition of flesh. Ideally each of these could be fully described over a range of environmental parameters such as temperature, oxygen levels, and feeding rates that affect the cultured species. Some of this information has been and is being developed within the OREHP project—in particular, information on the maintenance of spawning stock and growth and survival of the egg, larval, and juvenile stages. For older life history stages, information has been limited to observations of growth of captured individuals and growth data incidental to other experiments which may not reflect the potential growth rate of cultured fish. This presents a significant limitation to the precision of a detailed model, because costs are sensitive to growth rate. Preliminary estimates of parameters such as food conversion rates and tolerances for minimum dissolved oxygen levels and maximum ammonia concentrations have been taken from culture systems for similar species.

For many species, the aquaculture environment is adjusted so that growth rate is greater than that observed in the natural environment. Stephens et al.

(1988) in Table 7 of their annual report indicate growth rates of 0.019 and 0.028 cm/d for the first 97 d after hatching of California halibut at approximately ambient temperatures (16° C) and elevated temperatures (28° C) respectively. These growth rates are somewhat lower than estimates for the wild population but include the metamorphosis to the juvenile form during which the fish changes its shape significantly. Captured individuals raised in the laboratory yield similar growth rates (0.026 cm/d, Kaupp 1989 and 0.025 cm/d, Innis 1990) when raised over several years. The juvenile growth rates eventually attainable in an aquaculture system may be higher when the environmental requirements of the larval and juvenile stages are better known.

The nutritional energy requirements of fish can be partitioned into two categories: growth and maintenance. Maintenance requirements include basal metabolism and activities such as movement and feeding. For fish the caloric requirement for maintenance is commonly considered to be a power function of weight with the exponent falling between 0.6 and 0.8 and a coefficient dependent on activity level and body temperature. We have used a value of 0.69 for the exponent (from Townsend and Calow 1981, p. 27), and .05 kilocalories (kcal)/d for the coefficient in the power function. Schmidt-Nielsen (1979, p.186) gives a value of 0.001 kcal/h for poikilotherms at 20° C (for body weight in grams). However, this is a minimum estimate; active swimming can increase energy expenditures significantly. For the purpose of this model we have assumed a level twice the minimum.

In rapidly growing fish a large portion of the diet is used in growth. In aquaculture, growth is often expressed in terms of conversion efficiency, kilocalories of fish produced per kilocalorie of food. Food conversion efficiencies for cultured fish vary depending on species, feed type, and culture system. Typically, values of 1:3 or 1:4 (Bardach et al. 1972, p. 12) are considered to be very good. Reported values often include maintenance requirements. We use 1:3 in our standard model runs so that for each kilocalorie equivalent of weight gain the fish must be fed three times that many kilocalories of food. This is added to the energy required for maintenance to determine total food kilocalories in a time interval.

Oxygen requirements of cultured fish can be calculated using a mass balance equation by assuming that all food that is not converted to tissue is oxidized. Approximately 0.275 g of oxygen are required to metabolize each kilocalorie of food. Aeration requirements can be calculated as the difference between the available dissolved oxygen and this requirement. A value of 6.75 mg oxygen per liter is recommended as a minimum level that should be maintained for nonanadromous marine species (Poxton and Allouse 1982).

The most important waste product in this culture system will be ammonia. The effect of ammonia on the fish is dependent on temperature and pH because ammonia is only toxic in the unionized form. The unionized portion is sensitive to pH, being about 1% of total ammonia at a pH of 7 and 10% at a pH of 8 (Allen et al. 1984, p. 163). We have assumed an intermediate value of about 5% which corresponds to a pH of about 7.5. Increasing levels of ammonia first begin to inhibit growth, then at higher concentrations lead to mortality. For example, growth of Dover sole, *Solea solea*, and turbot, *Scophthalmus maximus*, were unaffected by unionized ammonia concentrations of around 0.1 mg/L, but levels of 0.3–0.9 mg/L prevented all growth (Poxton and Allouse

1982). Brownell (1980) found values of 24-h LC50 near 0.4 mg/L and values that inhibited first feeding >0.1 mg/L for marine fish larvae of several species. Setting the unionized ammonia tolerance at 0.1 mg/L yields a total allowable ammonia concentration of 2.0 mg/L.

Waste products are removed from a culture system with the waste water that flows out of the tanks. In a fish culture system, ammonia concentrations can be calculated using a mass balance equation involving the excess nitrogen in the feed (above that consumed by growth) and the inflow and outflow rate of water (Allen et al. 1984). Water flow rates can then be set so that ammonia is removed from of the system at the same rate that it is produced while maintaining the ammonia concentration in the tank below the critical concentration.

The composition of the food and the feeding rate affect growth and mortality rates directly but also determine the waste levels in the culture unit which affect the aeration requirement and water flow rate. A cost effective food composition should balance the nutrition requirements of the fish against the costs of waste removal and is necessarily species and culture system specific. We have limited the food composition parameters in the model to caloric content and ammonia equivalent. The feeding rate is calculated to satisfy the caloric requirements for growth and maintenance. We have arbitrarily set the feed parameters at an energy content of 5 kcal/g and an ammonia equivalent of 32 mg/g; these values are equivalent to a feed composed of 20% fat, 20% protein, and the rest carbohydrate (cf. Deniel 1976; Kuhlman et al. 1981).

The density of fish in the culture unit and the size and shape of the units affect growth and mortality rates in a complex and subtle manner. Optimal rearing densities are often dependent on poorly understood interactions such as the shape and water flow patterns of the tanks, the possibility of disease transmission, and species-specific behavioral patterns such as schooling, individual spacing, and cannibalism. Flat fish require a large benthic surface which places some constraints on the size and shape of the tanks. We have arbitrarily assumed the tanks to be 20,000 L; this corresponds to a tank 1 m deep by 6 m in diameter that is kept 3/4 filled. We have used tilapia and trout as representative of species for which densities have been optimized. Tilapia have been successfully reared at densities of 50 g/L of water (Ballerin and Haller 1982) and trout are reared at densities in excess of 10 g/L (cf. Leitritz and Lewis 1976). The number of tanks required is calculated to satisfy the biomass density criterion during the time step.

CULTURE AND FISHERY MODELS

To evaluate culture and fishery independently, then combine results, we divided the life history of a cultured, then stocked, fish into two phases. The point dividing these phases had to be greater than the maximum size to which fish would be cultured and less than the lower size limit of the current fishery. We chose this point somewhat arbitrarily to be 24 cm, which is a size at which the juveniles have typically left the nearshore environment. We refer to fish above this size as being in the potentially fishable population, and when we use the word "recruitment" we mean recruitment to this population. We stress that this is a somewhat arbitrary dividing point, and its exact value, as long as it is greater than the maximum culture size and less than the lower size limit in the fishery, will not affect the cost/benefit analysis. This separation results in three consecutive periods in the life history of a cultured, then stocked, fish: the culture phase, post-release phase, and post-recruitment phase (Figure 2). The first phase covers the period from hatching to release. The second phase covers the period from release to the size of recruitment into the potentially fishable population (24 cm), and the third covers the period from that size through adulthood and possible capture in the fishery. The specific release size can vary from post-larval size (i.e. no juvenile culture) to the size of recruitment into the fishable population (24 cm). During the time between release and the recruited size, fish are assumed to be in the "juvenile habitat" and are subject to different growth and mortality rates than after the recruited size when they are assumed to have adult growth and mortality rates.

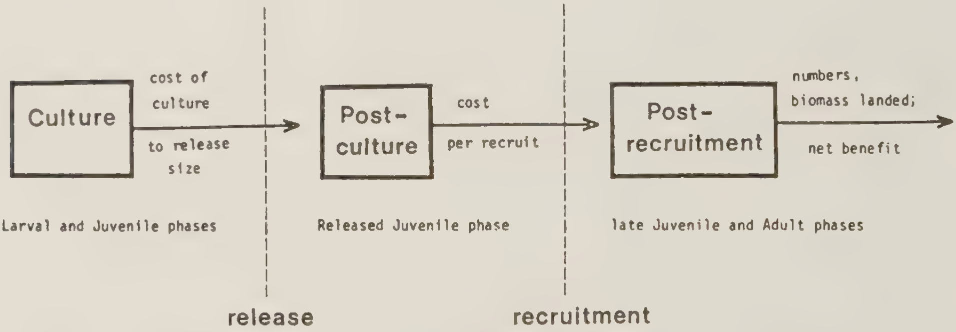

FIGURE 2. A schematic of the culture/release process as described in the computer programs for eocnomic evaluation.

Culture System Model

The model of the culture system has been developed to provide a means of examining the economics of culture based on the limited information presently available. The culture system model consists of three submodels: biological, physical, and economic (cf. Allen et al. 1984). The biological submodel defines the behavior of the fish in the environment of the culture system. The physical submodel is a description of the physical plant itself and the necessary inputs, and the economic submodel calculates the costs associated with running the culture system. The model is calculated iteratively. Each iteration represents a time step (usually 7 or 10 d) and begins with the growth of the fish. Then, using the growth, present size, and the environmental requirements of the fish, the necessary physical plant is sized and inputs are calculated. Finally, the costs are totaled to complete the iteration. The model is structured in this way to allow extrapolation of limited data for analysis over a wide range of size classes.

Biological Submodel

The biological model calculates growth and mortality during each time step. Growth in length is calculated as a function of time. We have used a linear model for increase in length so that,

$$L_{t+1} = L_t + (g_c \times \delta_t) \qquad (3)$$

with $L_0 = L_m$

where

L_t = length at time t

L_m = initial length

g_c = daily growth rate in the culture system

δ_t = time interval.

For our baseline model we have used approximately the estimated wild population growth rate (cf. Hammann and Ramirez-Gonzalez 1990) of g_c = 0.05 cm/d and an initial length of L_m = 2.5 cm.

Weight is calculated using the length-weight relation for the natural populations

$$W_t = w_c \times L_t^{w_e} \qquad (4)$$

where

W_t = weight at time t

w_c = weight-at-length coefficient

w_e = weight-at-length exponent

In our model we used the values given above computed from Hulbrock's (1974) data. Weight gain is the difference between weight at the beginning and end of the time step.

$$\delta_w = W_{t+1} - W_t = \text{weight gain per fish per time step} \qquad (5)$$

We use an exponential survival function so that

$$N_{t+1} = N_t \times \exp(-m \times \delta_t) \qquad (6)$$

where

N_t = number of fish at time t

m = mortality rate per day

In the baseline model the mortality rate m = 0.005/d.

Physical Submodel

The environmental variables—food, water flow rates, aeration requirement, and tank numbers—are calculated to meet the minimum caloric requirements for growth and maintenance, as well as maintain required dissolved oxygen levels, ammonia concentration and biomass density of fish.

The caloric requirements per time unit are partitioned into a growth requirement and a maintenance requirement that includes both basal metabolism and active swimming (Allen et al. 1984). Total food is calculated to meet these two needs as

$$F_t = \frac{(\delta_w \times k_b \times r_f) + (\delta_t \times b_c \times W_t^{be})}{k_f} \qquad (7)$$

where

F_t = weight of food required per fish per time step

k_b = kilocalories per unit of fish biomass

r_f = food conversion rate, kilocalories of fish gain per kilocalorie of food

b_c = maintenance coefficient

b_e = maintenance exponent

k_f = kilocalories per unit of food.

Using a mass balance equation, we calculate the oxygen required to metabolize all of the food, minus the amount which becomes fish biomass. It is

$$O_{2t} = [(F_t \times k_f) - (\delta_w \times k_b)] \times 0.275 \text{ g/kcal} \qquad (8)$$

where

O_{2t} = oxygen requirement per fish per time step

0.275 g/kcal = the amount of oxygen required to metabolize a specified amount of food.

The latter ratio (oxygen to energy) is for a hypothetical food which is 50% fat and 50% carbohydrate and protein by energy content. This constant is chosen conservatively so that the oxygen requirements of most common diet mixtures will be met. A higher fat content would require a higher rate but not greater than 0.30 g/kcal.

Ammonia production is also calculated from a mass balance equation as the amount of ammonia in the food, less that which becomes fish flesh. It is

$$NH_{3t} = (f_t \times n_f) - (\delta_w \times n_b) \qquad (9)$$

where

NH_{3t} = ammonia produced in time step t

n_f = grams of ammonia per gram of food

n_b = grams of ammonia per gram of biomass.

This assumes that all the nitrogen in food is excreted as ammonia or in a form that is converted to ammonia in the tank system. Because not all of the nitrogen is excreted as ammonia, it is a conservative (high) estimate.

For this evaluation, we have assumed a flow-through system with no water treatment. Water flowing through the system adds dissolved oxygen and removes ammonia. Flow rates must be set to provide a specified safe level of ammonia, but the additional required amount of oxygen can be met through aeration. Regardless of whether the tanks are aerated, the flow rate must be sufficient to prevent the ammonia concentration from exceeding a critical level. Flow per fish is

$$H_2O_t = \frac{NH_{3t} \times 2.0}{NH_{3c}} \qquad (10)$$

where

H_2O_t = total water required per fish in time step t

NH_{3c} = maximum allowable ammonia concentration.

Because of the variable nature of ammonia excretion due to noncontinuous feeding and incomplete mixing of water, we have included a safety factor of 2.0.

If the tanks are aerated, H_2O_t is the required flow rate per fish. If the tanks are not aerated, the dissolved oxygen in the inflowing water is assumed to be the primary source of dissolved oxygen in the system. The aeration deficit is calculated as

$$O_{2d} = \text{minimum } [H_2O_t \times (O_{2in} - O_{2c}) - (O_{2t} \times 2.0) \text{ or } 0.0] \qquad (11)$$

where

O_{2d} = deficit in grams of dissolved oxygen per fish per time step

O_{2in} = dissolved oxygen concentration in inflowing water

O_{2c} = minimum allowable dissolved oxygen concentration

minimum = function which selects the minimum of two values.

We have again included a safety factor of 2.0 to allow for the effects of imperfect mixing and nonconstant usage. If the oxygen deficit is zero, the flow necessary to remove the ammonia is satisfactory for the oxygen requirement as well. A nonzero oxygen deficit must be met by increasing the inflow of water, so that

$$H_2O_t = \frac{O_{2t} \times 2.0}{O_{2in} - O_{2c}}$$

The number of tanks required is based on a maximum biomass density criterion, so that

$$T_t = \frac{N_t \times W_t}{d_c \times t_v} \qquad (13)$$

where

T_t = number of tanks required at time t

d_c = maximum allowable density

t_v = tank volume.

Economic Submodel

The cost per individual entering the fishery is the total cost to raise a cohort divided by the number of that cohort that survive to enter the fishery. The total cost is the sum of the accumulated costs for food, electricity, water, and space. These are calculated on a per time step basis as the fish grow from post-larval size. We have not included economies of scale or discounting of future value.

The cost of food per time step for the cohort is

$$C_{ft} = F_t \times N_t \times P_f \qquad (14)$$

where

P_f = price per unit of food (\$/kg).

The cost of electricity per time step for the cohort is

$$C_{et} = (H_2O_t \times N_t \times H_2O_e) + (T_t \times T_e) \times P_e \qquad (15)$$

where

H_2O_e = electrical use per unit water (pumping)

T_e = electrical use per tank (lights, aeration, circulation pump)

P_e = price per unit of electricity (dollars/kw-h).

The cost of water per time step for the cohort is

$$C_{H2Ot} = H_2O_t \times N_t \times P_{H2O} \qquad (16)$$

where

P_{H2O} = price per unit of water (treatment, prorated pumps and piping).

The total capital cost during a time step is proportional to the number of tanks used during the time step, so that

$$C_{Tt} = T_t \times P_T \qquad (17)$$

where

P_T = price per tank per day (maintenance, labor, and prorated tank, building, and accessories).

The total accumulated cost of culturing a cohort up to age t is

$$C_{At} = C_{At-1} + C_{ft} + C_{et} + C_{H2Ot} + C_{Tt}, \quad (18)$$

beginning with the initial cost of the cohort (as either postlarvae or eggs),

$$C_{A0} = N_0 \times P_{pl} \quad (19)$$

where

P_{pl} = price per postlarva or egg.

Electrical use is calculated as that required to pump the total water flow 10 m vertically plus a fixed amount for lighting and aeration of tanks. The prices and parameter values are listed in Table 1.

Post-Release, Pre-Recruitment Model

The total accumulated cost of the cohort at age t is the total cost per stocked fish if the cohort is stocked at that age. However, the cost per recruit (24 cm) depends on the rate of survival to 24 cm as well as cost per stocked fish. The survival rate to recruitment depends on the time required to grow to the minimum entry size (24 cm) and the size-specific survival rate during that time. To describe post-release growth, we have used the linear growth model which is equivalent to growing the fish from post-larval size to the size at 1 year in the natural population over the span of 1 year, so that

$$t_L = \frac{L_r - L_t}{g_n} \quad (20)$$

where

t_L = time to reach the fishery

L_r = minimum length in the fishery (size at recruitment)

L_t = length at time of release

g_n = linear growth rate for the natural population.

For the baseline model we use the approximate estimated natural growth rate of juveniles (0.05 cm/d). We have assumed the mortality rate is a linear function of length in this phase. Because growth is linear, the rate is equal to the rate for the mean size during the time period prior to entering the fishery, so

$$m_L = m_p + \left[\left(\frac{L_t + L_r}{2} - L_p\right)\left(\frac{m_r - m_p}{L_r - L_p}\right)\right] \quad (21)$$

TABLE 1. Parameters and baseline values for culture system model.

Symbol	Parameter	Baseline value
L_m	Initial length, length of postlarva	2.50 cm
g_1	Growth rate	0.050 cm/d
δ_t	Time interval per time step	10 d
w_c	Coefficient for length to weight function	0.00872
w_e	Exponent for length to weight function	3.048
m	Mortality rate per day	0.005
k_b	Kilocalories per unit of fish biomass	1.3 kcal/g
r_f	Food conversion rate, kcal of fish gain per kcal of food	0.30
b_c	Coefficient in basal maintenance function	0.05
b_e	Exponent in basal maintenance function	0.69
k_f	Kcal per unit of food	5.0 kcal/g
n_f	Ammonia concentration in food	0.032 g NH3/g
n_b	Ammonia per gram of fish biomass	0.016 g NH3/g
NH_{3c}	Maximum allowable ammonia concentration	0.10 mg/L
O_{2in}	Dissolved oxygen concentration in inflowing water	8.0 mg/L
O_{2c}	Minimum allowable dissolved oxygen concentration	6.75 g O_2/L
d_c	Maximum allowable biomass density	50.00 g/L
t_v	Volume of tanks	20000 L
P_f	Price per unit of food	$ 1.00/kg
H_2O_e	Electrical use per unit of water	0.03 kwh/1000 L
T_e	Electricity used per tank	7.0 kwh/tank/d
P_e	Price per unit of electricity	$ 0.10/kwh
P_{H2O}	Price per unit of water	$ 0.00/1000 L
P_T	Prorated price per tank per day	$ 3.50/tank
N_0	Initial number of post-larval fish	100,000
P_{pl}	Price per post-larval fish	$ 0.15/postlarva
L_r	Length at recruitment	24.00 cm
g_n	Linear growth rate for the natural population	0.05 cm/d
m_r	Instantaneous yearly mortality rate at recruitment	0.3/year
m_p	Instantaneous yearly mortality rate at post-larval size	7.0/year

where

L_p = length of post-larval fish

m_L = average mortality rate for fish growing from L_t to L_r

m_r = instantaneous yearly mortality rate at size of recruitment

m_p = instantaneous yearly mortality rate at post-larval size

For the mortality rate at post-larval size we use $m_p = 7.0$/year, and for the mortality rate at recruitment we use $m_r = 0.3$/year, the baseline value of natural mortality of adult fish.

The survival rate for the period from stocking to recruitment into the fishable population for fish of size L is

$$S_L = \exp(-m_L \times t_L) \qquad (22)$$

and the cost per fish stocked at time t that will actually reach recruitment is

$$C_{rt} = \frac{C_{at}}{S_L \times N_t} \qquad (23)$$

Post-Recruitment, Fishery Model

The post-recruitment fishery model must describe the bioeconomic dynamics of stocked fish after recruitment to the potentially fishable stock so that the economic benefit of the culture/stocking program can be evaluated. These dynamics depend on individual growth and mortality, as well as how the fishery is managed (i.e. the size limit and mortality due to fishing; c.f. Botsford and Hobbs 1984). Because yearly fishing mortality rates are poorly known and we may wish to examine possible benefits of changes in management, we evaluate the benefits of stocking over a range of fishing mortality rates and size limits. We consider here only a single fishery. This can be thought of as the combined recreation and commercial fishery. For a more detailed analysis of the catch distribution among multiple users with use-specific regulations, see Reed and MacCall (1988).

The impacts of stocking on the fishery can be separated into two areas: the direct, short-term impact and the indirect, long-term impact. The former includes effects of stocked fish entering the fishery and the latter includes the effects of descendants of stocked fish entering the fishery. Because prediction of the indirect, long-term impacts requires knowing the processes that control recruitment, we concern ourselves here with only the direct, short-term effects.

Several aspects of the post-recruitment dynamics are of potential economic interest. The most obvious characteristic is fishery catch per stocked fish both in numbers and in biomass. These depend only on post-recruitment growth and mortality rates, however, and do not reflect culture costs. Another way of looking at the post-recruitment effects of stocking, therefore, is in terms of the cost per fish caught. To account for the size and value of the fish caught, a fourth way of evaluating stocking is in terms of net value (gross value minus cost) of fish caught, assuming gross value of a fish is proportional to weight.

The model assumes that yearly mortality rates (both fishing and natural) are constant and that growth follows a von Bertalanffy curve. The number of recruits at any age past recruitment is

$$N_t = N_0 \times S_t \qquad (24)$$

where

N_t = number of fish at time t

N_0 = number of fish at time 0 (recruitment or age 1)

S_t = portion surviving from recruitment.

Survival prior to entering the fishery is given by

$$S_t = \exp(-m \times t) \qquad \text{for } t \leq t_c \tag{25}$$

where

m = instantaneous yearly natural mortality rate

t_c = time at which fish reach the minimum size limit.

We use an intermediate value of 0.2/year as a baseline for our analysis here but also evaluate the sensitivity of the results to a range of values from 0.1 to 0.3/year. Botsford et al. (1989) presented results for a more conservative analysis using a mortality rate of 0.3/year. After the age of entry into the fishery

$$S_t = \exp[-(m \times t) - (f \times [t-t_c])] \tag{26}$$

where

f = instantaneous yearly fishing mortality rate.

Catch per recruit is the fraction of recruited, stocked fish (numbers) caught in the fishery. This is calculated as

$$c_r = \frac{f}{m+f} \times \exp\ (-t_c \times m). \tag{27}$$

Biomass yield per recruit is the average weight increase in the total catch per recruited, stocked fish (biomass). The yield is calculated by numerical integration from

$$Y_r = \frac{f}{m+f} \int_0^\infty S_t W_t \, dt \tag{28}$$

where

$W_t = a_1 \times L_t^{b_1}$ = weight in kilograms at time

a_1 = the coefficient in the length-weight relationship

b_1 = the exponent in the length-weight relationship

$L_t = a_2 \times [1-\exp(-b_2 \times [t-c_2])\,]$ = length in cm.

For the parameters in the von Bertalanffy growth equation (a_2, b_2, and c_2), we used values estimated from Hulbrock's (1974) data.

Culture cost per fish caught is calculated as

$$P_f = \frac{P_r}{C_r} = \frac{\text{cost per recruit}}{\text{catch per recruit}} \tag{29}$$

and net benefit of yield per recruit is

$$B_r = (p_k \times Y_r) - P_r = \text{value of yield per recruit} - \text{cost per recruit} \quad (30)$$

where

p_k = value per unit weight of fish to the fishery in \$ /kg

P_r = cost per recruit, obtained from the culture cost model.

RESULTS

Our analysis thus far is limited by the results available from culture research. We have developed an understanding of the dynamics of the culture/stocking system (i.e. how the system "works") and a preliminary estimate of culture costs and benefits. We have also identified aspects of the system to which costs are particularly sensitive and used these sensitivity analyses to evaluate results from biological experiments. The third category can be useful in planning future research. Cost or benefit figures should be considered preliminary at this stage.

Culture

The simplest view of how a culture system would work can be obtained by following the development of a cohort of fish as they grow through culture (Table 2). As the fish increase in size, the number of tanks required increases even though the number of fish declines because of mortality. Costs per time step increase as the fish increase in size and metabolic demand, and the total cost of culture per fish begins with the cost per postlarva and increases to higher values. For purposes of determining the sensitivity of culture costs to changes in the system due to further research, it is valuable to know the distribution of costs. Early in culture the costs of post-larval fish dominate total costs, but they constitute a lower proportion relative to costs of food, labor, and the physical system as fish are cultured longer (Figures 3 and 4).

Optimal Size of Release

A critical open question with regard to the culture/stocking system is how long the fish should be cultured before being released. Shorter culture time will incur less culture costs, but fewer fish will survive after release to be fishable recruits. The number that survive depends on juvenile mortality rate which decreases with age and size of the fish. Consequently, there is a tradeoff between the increased cost of larger fish and the decreased survival of smaller fish (Figure 5; see Table 1 for parameter values). As the possible release size increases, both the cost per fish released and the fraction that would survive to recruitment size increase, but at different rates. The cost per recruit is the cost per fish released divided by the survival to recruitment (23)]. This value initially declines, then increases, and the optimal size of release is the minimum of this curve. For example, Figure 5 indicates that to minimize overall cost per cultured

TABLE 2. Culture plant simulation program.

Age (days)	Average length (cm)	Total dry weight of food fed per day	Daily costs during time step	Survival from initial post-larval stock	Number tanks required	Average weight
0	2.50	0.000	4.20	1.000	1	0.142
10	3.00	0.013	6.84	0.951	1	0.248
20	3.50	0.018	7.71	0.905	1	0.397
30	4.00	0.024	8.65	0.861	1	0.596
40	4.50	0.031	9.65	0.819	1	0.854
50	5.00	0.039	10.70	0.779	1	1.178
60	5.50	0.048	11.77	0.741	1	1.574
70	6.00	0.058	12.87	0.705	1	2.053
80	6.50	0.069	13.97	0.670	1	2.620
90	7.00	0.080	15.07	0.638	1	3.284
100	7.50	0.093	16.17	0.607	1	4.052
110	8.00	0.106	17.25	0.577	1	4.933
120	8.50	0.121	18.30	0.549	1	5.935
130	9.00	0.136	19.33	0.522	1	7.064
140	9.50	0.153	20.33	0.497	1	8.329
150	10.00	0.170	21.29	0.472	1	9.739
160	10.50	0.189	22.21	0.449	1	11.301
170	11.00	0.208	23.09	0.427	1	13.022
180	11.50	0.228	23.92	0.407	1	14.912
190	12.00	0.250	24.71	0.387	1	16.977
200	12.50	0.272	25.45	0.368	1	19.226
210	13.00	0.295	26.15	0.350	1	21.668
220	13.50	0.319	26.79	0.333	1	24.309
230	14.00	0.345	27.39	0.317	1	27.159
240	14.50	0.371	27.94	0.301	1	30.225
250	15.00	0.398	28.44	0.287	1	33.515
260	15.50	0.426	33.09	0.273	2	37.038
270	16.00	0.455	33.50	0.259	2	40.801
280	16.50	0.486	33.86	0.247	2	44.813
290	17.00	0.517	34.18	0.235	2	49.082
300	17.50	0.549	34.45	0.223	2	53.616
310	18.00	0.582	34.68	0.212	2	58.423
320	18.50	0.616	34.87	0.202	2	63.512
330	19.00	0.652	35.02	0.192	2	68.890

Release size to minimize cost per rec. = 17.00 cm
Release age to minimize cost per rec. = 290.00 days
Cost per released fish at optimum = 0.89557549 $/release
Minimized cost per recruit = 1.52805835 $/recruit

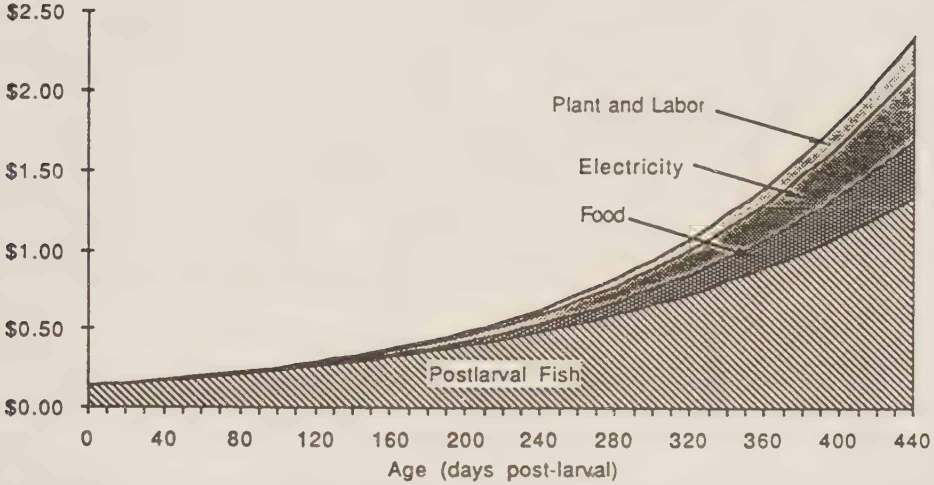

FIGURE 3. Distribution of costs per released fish by age at release in terms of actual value.

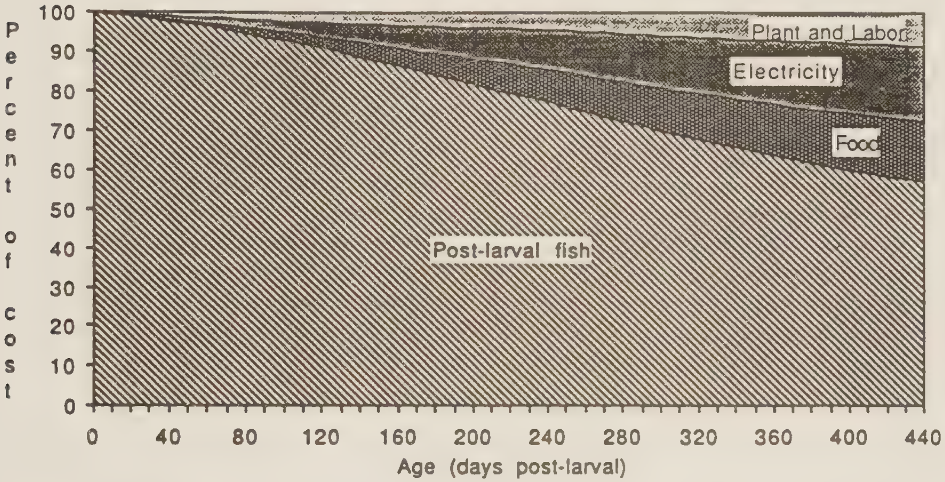

FIGURE 4. Distribution of costs per released fish by age at release as a proportion of total cost.

recruit, the cultured fish should be released after about 290 d of culture. The value of optimal release is sensitive to both the initial cost of post-larval fish and to the post-release survival rates.

Graphical Analysis of Sensitivity

Because of the preliminary nature of the research into culture of the post-larval fish, there is a great deal of uncertainty regarding the food characteristics and the culture units (tanks) necessary. Also, the growth rates observed in the culture system are lower than those observed in the wild population. We have therefore evaluated the sensitivity of culture-system performance to these parameter values. This is most easily done graphically.

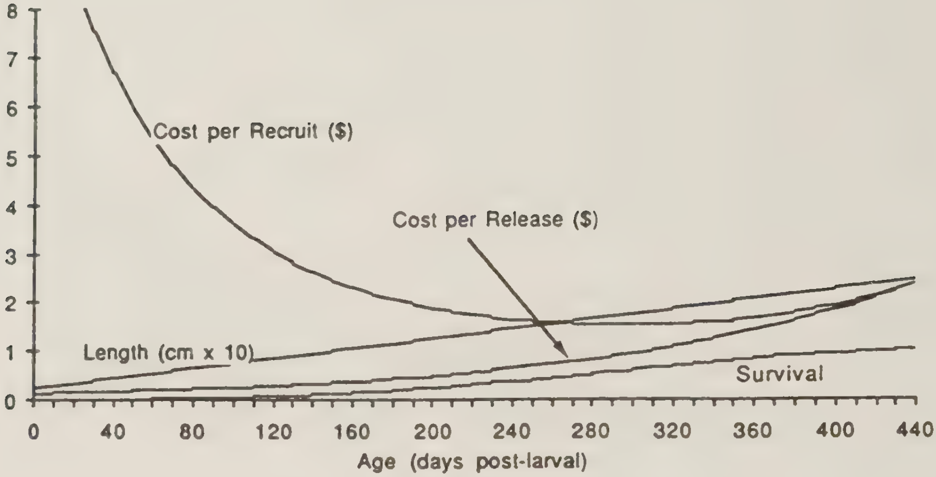

FIGURE 5. Cost per recruit (at 24 cm) if released from culture at the age on the horizontal axis. Other lines are the components of this cost (Equation 23).

Culture costs and operation of the culture system are sensitive to growth rate. We compare cost per recruit for six different values of growth rate in the culture plant (Figure 6). These lines are the same as the cost-per-recruit line in Figure 5 for different values of individual growth rate. Note that both the optimal time of release and the resulting cost per recruit are sensitive to this parameter. Little benefit would be gained by culturing the fish at growth rates less than 0.02 cm/d, and at rates as low as 0.01 cm/d continuing culture beyond the post-larval phase would increase the cost per recruit. Recall 0.025 cm/d is the highest observed laboratory growth rate and 0.05 cm/d is the estimated wild growth rate. This figure shows that for both of these values culture beyond the post-larval phase is optimal, but that the cost per recruit is high (e.g. for the former value, cost per recruit is near $5.00).

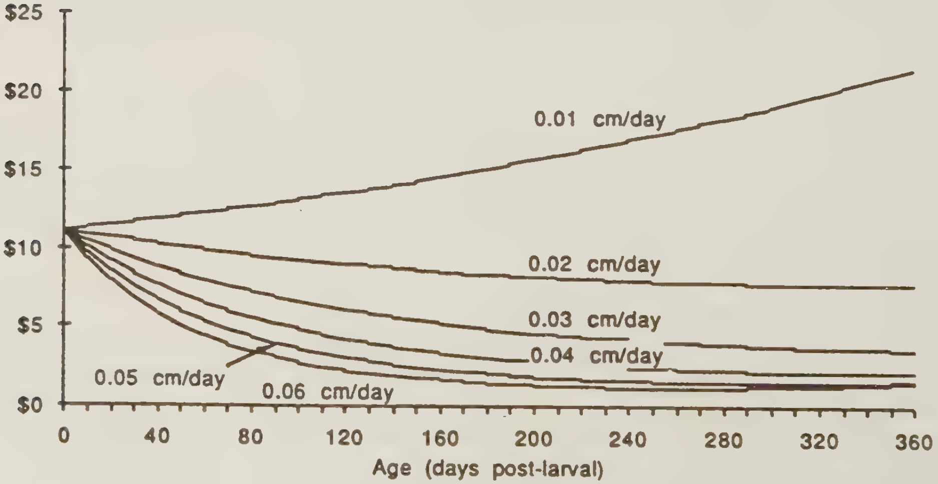

FIGURE 6. Cost per recruit as in Figure 5 for several different values of growth rate in culture.

Daily food costs and culture tank costs increase as the fish grow. Increases in the price of each of these has a significant affect on both the optimal release age and the cost per recruit (Figures 7 and 8). As food costs increase, cost per recruit increases, and the optimal release time decreases. The cost of tanks has a similar effect. Gadomski et al (1990) state that they have not been able to find a prepared food that post-larval halibut will utilize. Live food either collected or cultured is generally more expensive than prepared foods. Increased food costs would result in a younger optimum release age and a higher cost per recruit, but culturing beyond the post-larval phase is still cost effective in the sense that cost per recruit is less (but still expensive). A similar result occurs when cost per culture unit is varied.

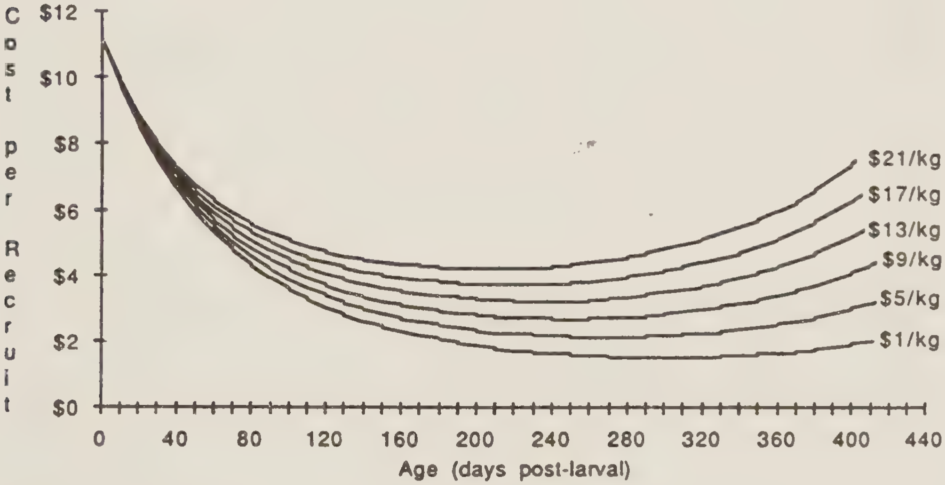

FIGURE 7. Cost per recruit for different food prices.

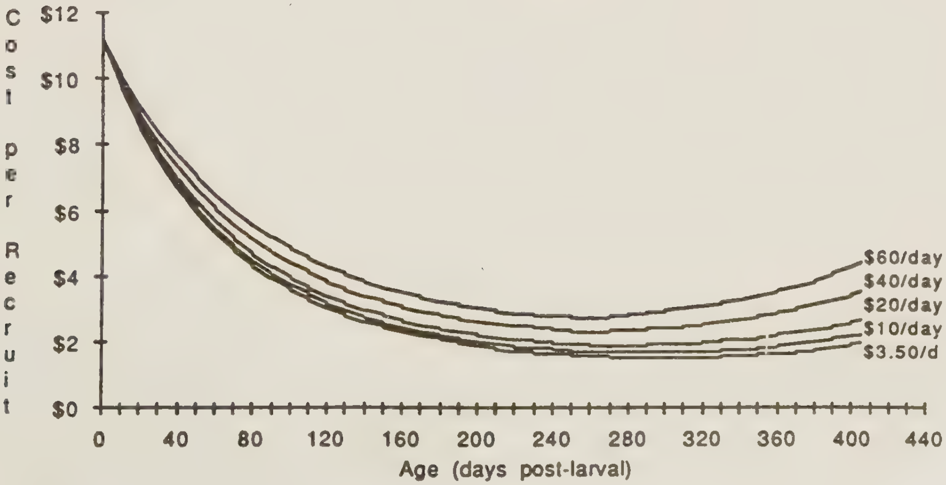

FIGURE 8. Cost per recruit for different costs of culture space.

Using increased food price as a typical increase in culture costs, we can examine the interaction of growth rate and culture costs (Figure 9). Even at high daily culture costs (food price of $50.00/kg) the optimal release age is greater than zero when the growth rate is greater than 0.02 cm/d. Minimized cost per recruit when compared for the same values of growth rates and food prices indicates that at growth rates above 0.02 cm/d the minimized cost per recruit is sensitive to food price (Figure 10). For lower growth rates no further culture of postlarvae is warranted even at very low food prices, so minimized cost per recruit is the cost of stocking postlarvae. Expensive culture practices may be cost effective if they increase the growth rate significantly. For example, food that cost $30.00/kg but increased the growth rate to 0.06 cm/d would result in a slight savings over $1.00/kg food that resulted in a growth rate of 0.025 cm/d, and a food that cost $10.00/kg with a potential growth rate over 0.04 cm/d would cut the minimized cost per recruit in half. Finally it should be noted that large increases in culture costs (e.g. 50-fold increase in food price) do not result in equivalent increases in minimized cost per recruit (approximately five fold), because a compensatory decrease occurs in optimal release age (Figures 9 and 10).

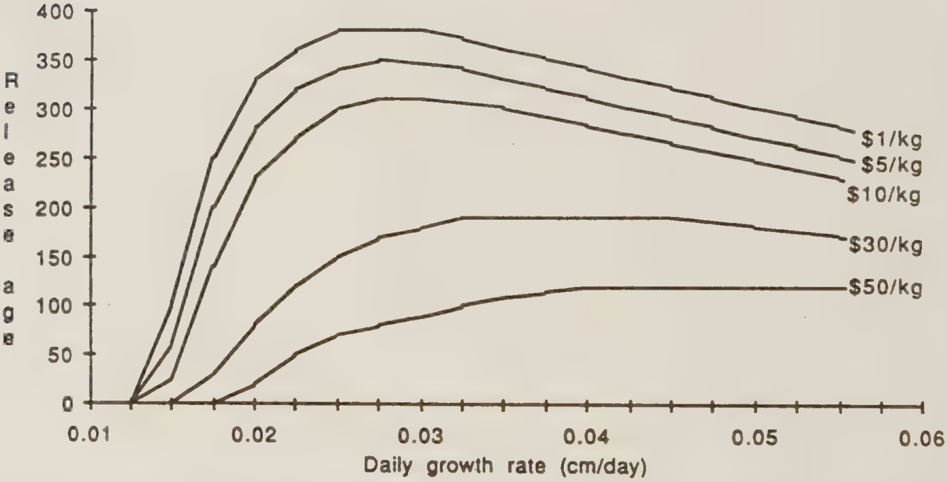

FIGURE 9. Optimal release age as both the cost of food and one of the potential effects of different foods, growth rate, vary.

Post-release mortality rates are also poorly known. In the model the post-release mortality parameter with the greatest uncertainty is the mortality of a post-larval fish (recall that post-release mortality rate is size dependent and decreases linearly from the post-larval size to recruit size, hence this is the value at lower end of this size range). Optimal release size, age, and cost, and the resulting cost per recruit, all increase with this parameter (Figure 11). The optimal values of these variables are those that correspond to the release age at which cost per recruit is minimized. The value of mortality rate used in the

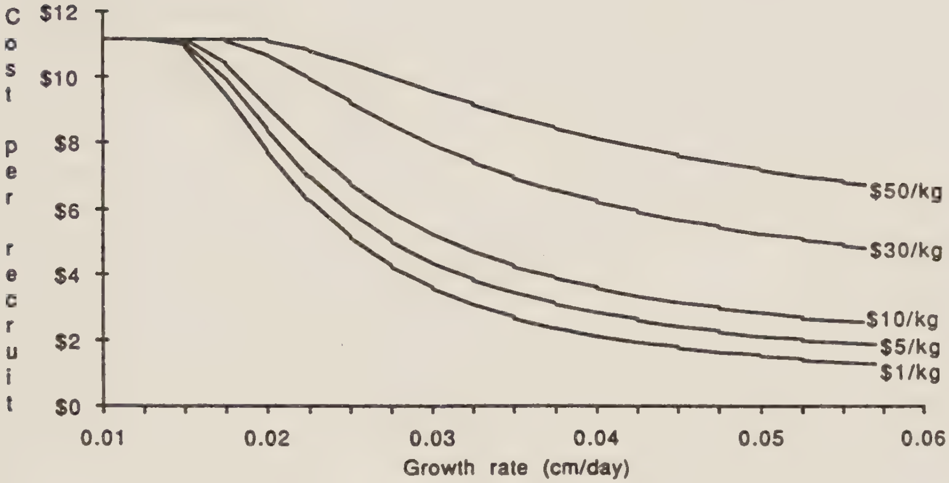

FIGURE 10. Cost per recruit (at 24 cm) as both the cost of food and growth rate vary.

baseline model is an instantaneous yearly rate of 7.0/year which would result in 1.3% survival from the post-larval size of 2.5 cm to the recruitment size of 24 cm. It is somewhat surprising to note that the cost per recruit varies relatively little (from $1.30 to $1.72) when the mortality rate is varied by a factor of two (from 5.0/year to 10.0/year or survival of 4.4% to 0.2% respectively). The cost per released fish varies by a factor of two (from $0.64 to $1.25), so the relative insensitivity of the cost-per-recruit variable results from an adjustment of the optimal release age (240 d to 340 d) that partly compensates for the variation in mortality rate.

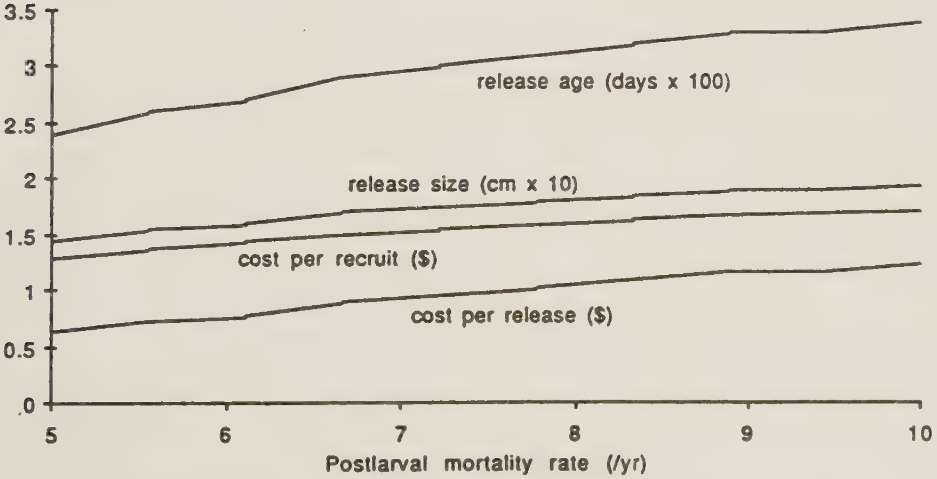

FIGURE 11. Optimal release age and size, and the associated cost per released fish and cost per recruit (at 24 cm) as the early natural mortality rate of juveniles is varied.

One question that would arise from Figure 11 is how sensitive cost per recruit is to changes in both parameters of the post-release mortality rate (i.e. both the post-larval value and the pre-recruit value). Even when both parameters are varied, one by a factor of two and the other by a factor of six, the cost per recruit varies only from $1.19 to $1.84 (Figure 12).

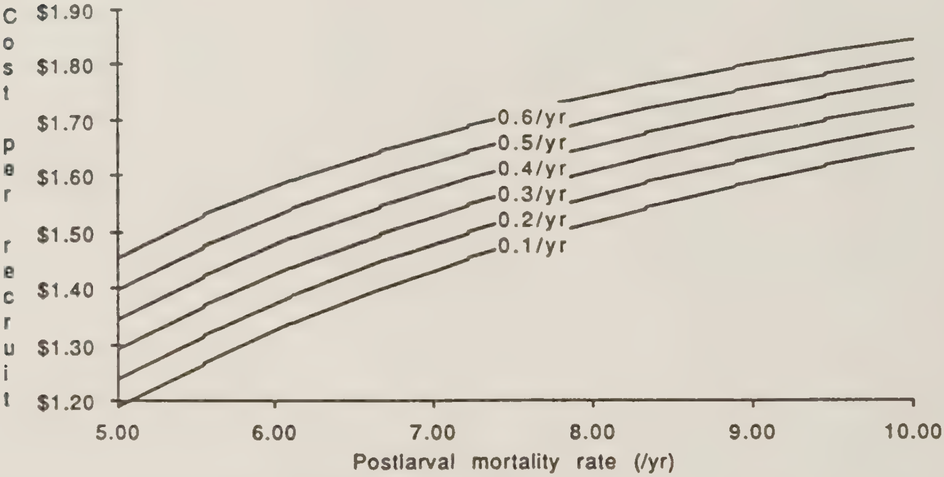

FIGURE 12. Cost per recruit as both the post-larval mortality rate (horizontal axis) and pre-recruitment mortality rate (individual lines) are varied.

Post-Recruitment

Direct, short-term impacts of the stocking program are evaluated here in four different ways. Parameter values used are shown in Table 3. These results are presented for a range of lower size limits and fishing mortality rates so that both the sensitivity of results to poorly known fishing mortality rates and the possible effects of changes in fishery policy can be evaluated.

The fraction of recruited, stocked fish that ends up being caught increases with the amount of fishing (i.e. the fishing mortality rate) because fewer fish survive long enough to die from natural mortality (Figure 13). It also increases as the size limit is lowered because fewer fish die from natural causes before reaching legal size. To get an idea of what would result from current management, we can look at the current size limit of 55.9 cm and assume a total fishing mortality rate including both sport and commercial fishing of 0.25/year; the fraction caught would be 0.22. This depends critically on stocked fish having the same survival rate as that estimated for natural fish (see Table 3).

Biomass caught accounts for the fact that fish grow larger with age while the fraction caught declines. The catch in the fishery in terms of biomass per recruited, stocked fish is higher at higher fishing rates and at intermediate size limits (Figure 14). Near 55.9 cm and 0.25/year it is relatively flat, indicating that little would be gained by a change in fishery policy and that, even if our

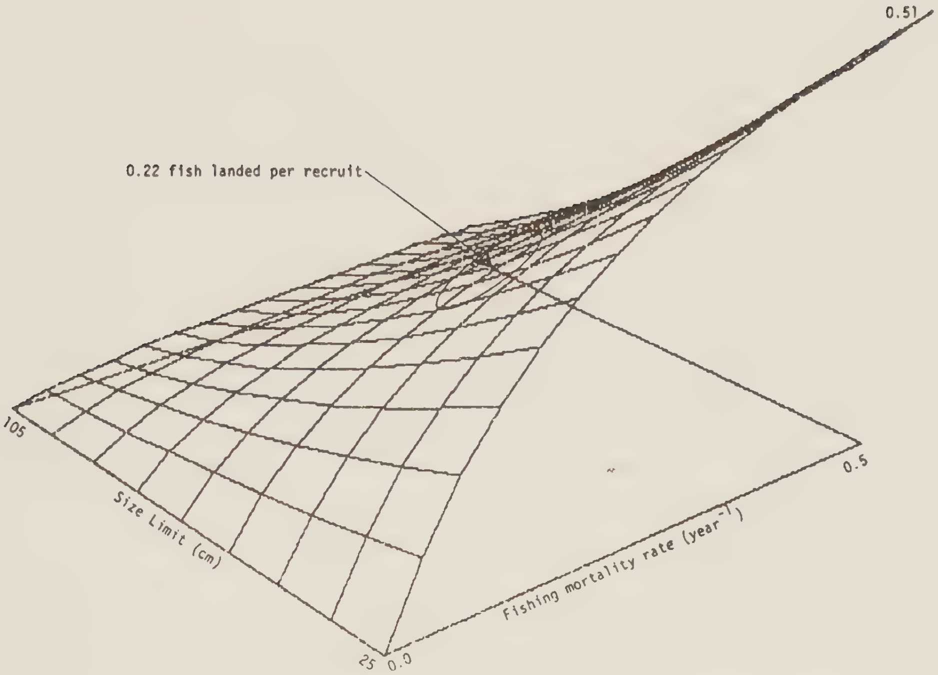

FIGURE 13. Fish landed per California halibut recruit as size limit and fishing mortaility rate are varied. The area marked corresponds to the present fishery.

TABLE 3. Parameters and values for post-recruitment model for California halibut

Symbol	Parameter	Value
m	Natural mortality rate	0.20/yr
a_1	Coefficient of length to weight (cm to kg) function	0.872×10^{-5} kg
b_1	Exponent for length to weight (cm to g) function	3.048
a_2	Maximum length (for Von Bertalanffy length at age)	128.5 cm
b_2	Growth parameter (for Von Bertalanffy length at age)	0.1207/yr
c_2	Age at length zero (for Von Bertalanffy length at age)	0.0983 yrs
P_r	Culture cost per recruit	$1.13/recruit
p_k	Value per kilogram of fish caught in fishery	$4.00/kg

estimates of fishing mortality rate are off a bit, our projected biomass yield will not be far off. The value at that point is approximately 0.93 kg.

The two criteria evaluated thus far do not include the costs of stocking. The cost per stocked fish caught for California halibut is shown for various values of fishing rate and size limit in Figure 15. For low fishing rates and high size limits, this criterion is high (because few fish are caught). However, near the current operating point the cost is about $5.05 for a landed fish that would average 4.2 kg (yield per recruit / fraction caught). This cost could be reduced by lowering the size limit, but that would lead to smaller fish in the catch.

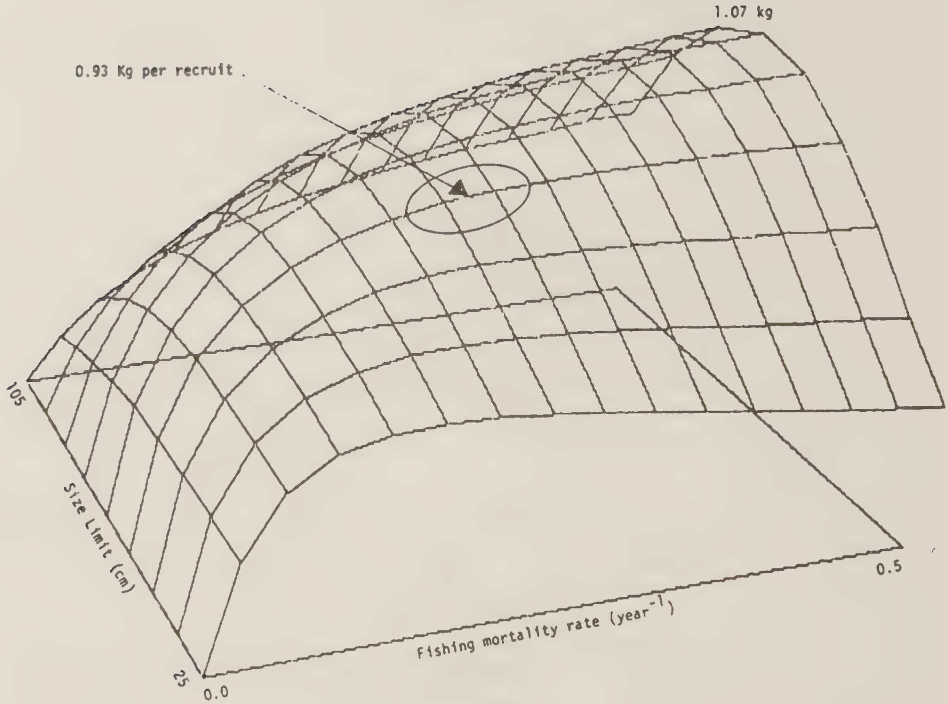

FIGURE 14. Biomass yield per California halibut recruit as size limit and fishing mortality rate are varied. The area marked corresponds to the present fishery.

A way of including the size of the fish in an economic criterion is to compute the difference between value to the fisherman (assuming it is proportional to weight) and the cost of culturing the fish. Net benefit is shown in Figure 16 for a value of $4.00/kg. This increases with fishing rate then decreases slightly and is a maximum for intermediate size limits. At the current operating point the net benefit is about $2.84 per recruit. The curve is fairly flat in the vicinity of this point.

A characteristic common to all of the four criteria is that they are sensitive to the assumed value of natural mortality rate. As one moves from a low estimate of 0.1/year to a high estimate of 0.3/year, biomass yield per recruit declines from 2.40 kg to about 0.43 kg (Figure 17) and the cost per stocked recruit caught increases from $2.50 to about $10.00 (Figure 18).

CONCLUSIONS FROM ANALYSES TO DATE

The analyses, thus far, raise some important issues that are worthy of attention. With regard to the culture phase, the fact that the cost of post-larval fish may dominate costs is important. For the analyses described here, we used a price ($0.15) which is less than the cost of commercially produced postlarvae of striped bass, *Morone saxatilis,* (for which females are also captured, and

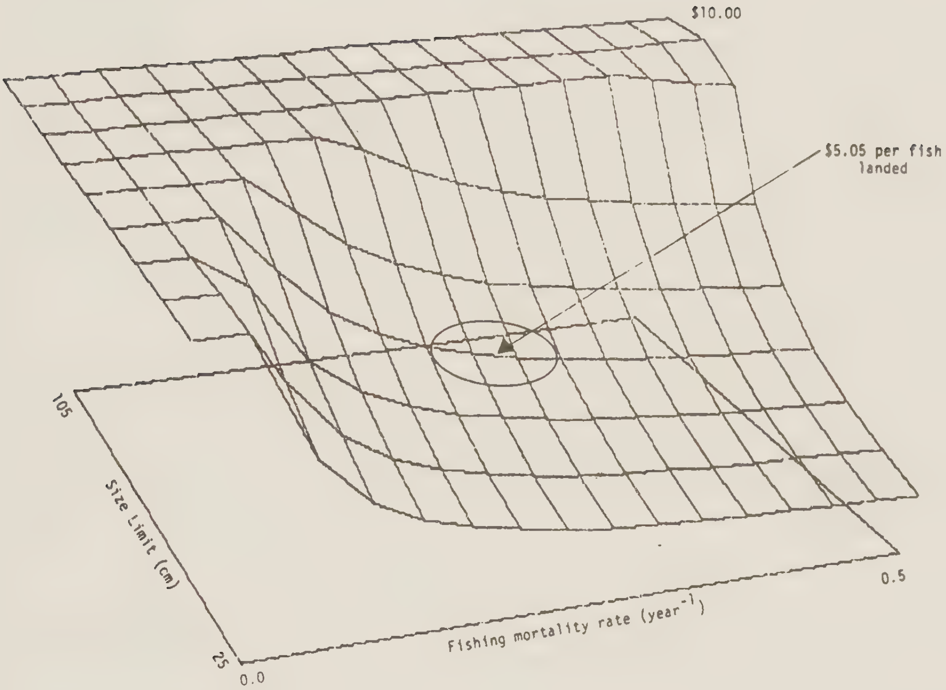

FIGURE 15. Average cost per stocked California halibut recruit as size limit and fishing mortality rate are varied. The area marked coresponds to the present fishery.

postlarvae are also reared from eggs). Using this value, costs of postlarvae are a major part of culture costs. This would imply that more attention should be paid to reducing this cost. Also, an accurate estimate of these costs is necessary because of its effect on the decision regarding optimal time of release.

A graph such as Figure 5 is the best single summary of how the culture/stocking scheme works. The variation in cost per recruit as time of release from culture increases, indicates the optimal time of release, as well as the penalty for early or late release. It is somewhat surprising that cost per recruit is relatively insensitive to post-release mortality (Figure 11, 12). However, this result assumes that we know the post-release mortality rates, and can release the cultured fish at the optimal release time. It will be advisable to monitor survival during the post-release/pre-recruit period, and to continue to refine optimal release time, even after the project begins releasing cultured fish.

Figure 5 can be used to evaluate some of the recent conclusions by the halibut culture researchers. For example, the annual progress report for 1987–88 for California halibut (Stephens et al. 1988) stated that the best release age was 6 to 7 weeks, primarily because of lack of an available food and space limitations in culturing a bottom dwelling fish. However, modeling results described here indicate the cost per recruit at this age would be about $6.00 per fish (Figure 5). Thus, it appears that release at this age is not economically feasible, and that further research isrequired to develop the capability of

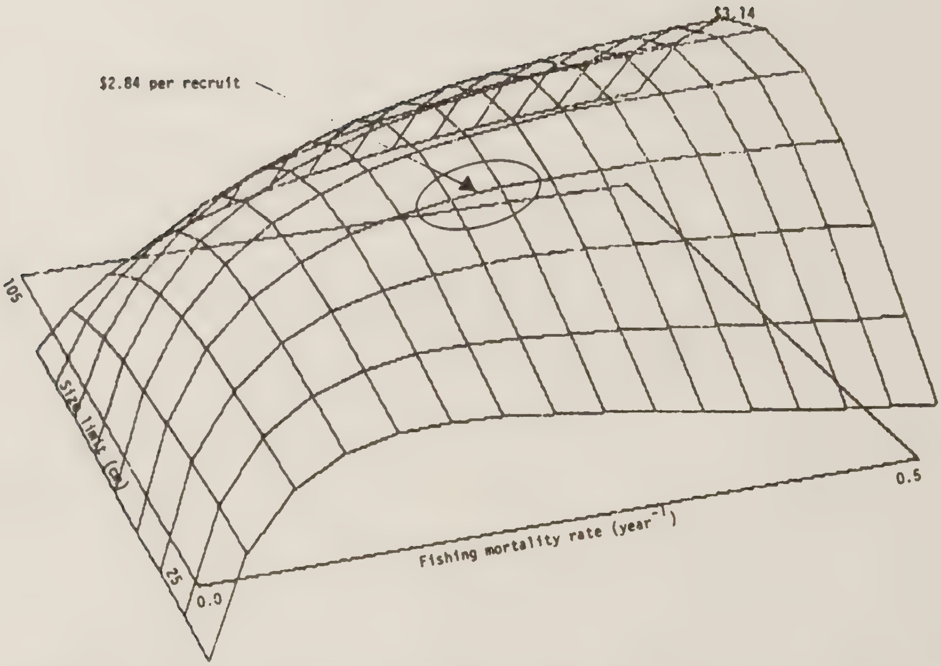

FIGURE 16. Net benefit per stocked California halibut recruit as size limit and fishing mortality rate are varied. The area marked corresponds to the present fishery.

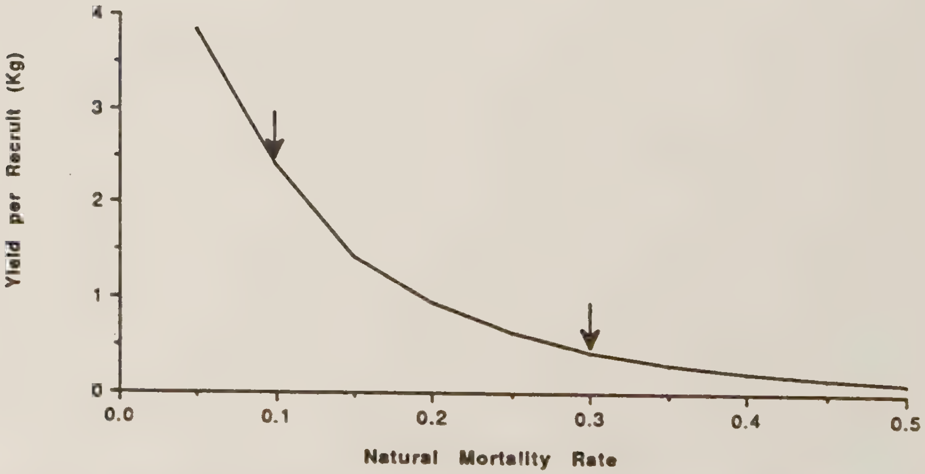

FIGURE 17. Biomass yield per California halibut recruit as natural mortality rate is varied. Arrows indicate recent low and high estimates of natural mortality rates.

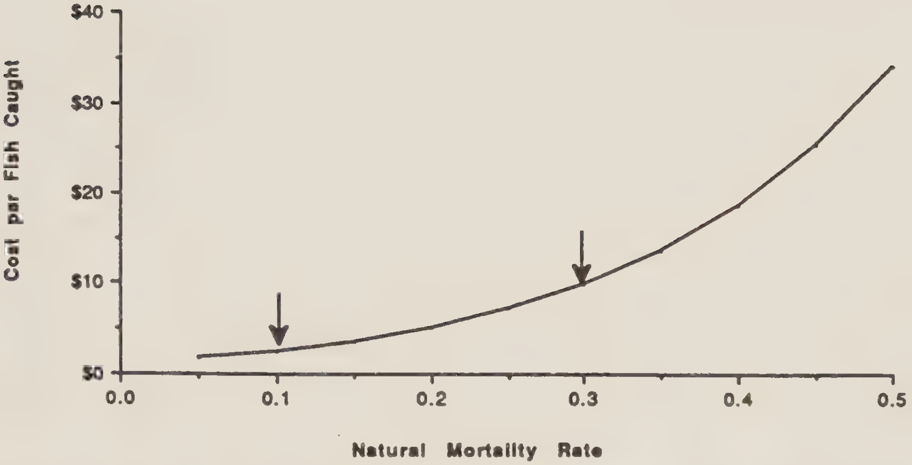

FIGURE 18. Average cost per stocked California halibut recruit caught in the fishery as natural mortality rate is varied. Arrows indicate recent low and high estimates of natural mortality rates.

culturing these fish to older ages. The economic analysis indicates that costs for food and culture space can be much higher than our baseline estimates and still result in substantial savings with culturing to an older release age (Figures 7 and 8). Other flatfish species have been cultured to larger sizes (Bardach et al. 1972).

Figure 6 reflects the implications of the current halibut growth rate. If growth rates are less than 0.02 cm/d, culture is not optimal (i.e. the optimal age of release is zero). If the growth rate is about 0.025 cm/d, the cost per recruit is about $8.00. A growth rate approximating the wild growth rate (0.05 cm/d) is required to bring the cost per recruit down to about $1.50.

The post-recruitment analysis provides an understanding of the economics of the culture/stocking system in terms of the fishery. We do not yet have the data necessary to confidently estimate culture costs, but the results illuminate sensitivity to various parameters. For example, they emphasize the importance of natural mortality rates. All criterion were sensitive to the value of that parameter. For California halibut the value probably lies between 0.1/year and 0.3/year, but this limited range allows a large uncertainty in the feasibility analysis. Because of the difficulty in estimating mortality rates in natural populations (Vetter 1988), some uncertainty will always be present in evaluations of the feasibility of the culture/stocking scheme.

Implications of current model results for feasibility of the culture/stocking concept are not straightforward. Cost and benefit projections appear high (about $5 per fish caught and a net benefit of $3 per fish if their value is $4/kg). However, these are based on growth at a rate near the natural rate to optimal release size. This growth rate is greater than current rates in culture and the optimal release size is far beyond the size to which researchers have thus far been able to grow this fish. If released at that size, cost per fish caught would be about $18, a value that is probably too high.

Overall evaluation of feasibility would also include consideration of less tangible effects of culture that are not included in our analysis. One example is the contribution of cultured fish to future recruitment. This would presumably be positive; however, there might be negative effects on genetic variability. Another less tangible effect is the negative effect that culture might have on the ability to protect habitat in the future. Some might assume that because fish could be cultured, there was less reason to protect natural spawning habitat.

ACKNOWLEDGMENTS

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LITERATURE CITED

Allen, P.G., L.W. Botsford, A.M. Shuur, and W.E. Johnston. 1984. Bioeconomics of aquaculture. Elsevier. 351 p.

Ballerin, J.D. and R.D. Haller. 1982. The intensive culture of tilapia in tanks, raceways and cages. Pages 265–356 *in* J.F. Muir and R.J. Roberts, eds. Recent Advances in Aquaculture. Crown Helm Ltd., London.

Bardach, J.E., J.H. Ryther, and W.O. MacLarney. 1972. Aquaculture: the farming and husbandry of freshwater and marine organisms. Wiley-Interscience, New York. 868 p.

Barry, J.P. and G.M. Cailliet. 1981. The utilization of shallow marsh habitats by commercially important fishes in Elkhorn Slough, California. Pages 38–47 *in* D. Koch, ed. Cal-Neva Wildlife Transactions, 1981.

Barsky, K.C. 1990. History of the commercial California halibut fishery. Pages 217–227 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Botsford, L.W. and R.C. Hobbs. 1984. Optimal fishery policy with artificial enhancement through stocking: California's white sturgeon as an example . Ecological Modeling. 23:293–312.

Botsford, L.W., R.C. Hobbs, and R.G. Kope. 1989. Bioeconomic evaluation of the culture/stocking concept for white seabass and California halibut: models and computer programs. Final Report. OREHAP Project. Calif. Dept. Fish and Game. Mimeo. 81 p.

Brownell, C.L. 1980. Water quality requirements for first-feeding in marine fish larvae. I. ammonia, nitrite, and nitrate. J. Exp. Mar. Biol. Ecol. 44: 269–283.

Clark, G.H. 1931. The California halibut (*Paralichthys californicus*) and an analysis of the boat catches. Calif. Dept. Fish and Game, Fish Bull. 32. 54 p.

Deniel, C. 1976. Growth of 0-group turbot (*Scophthalmus maximus* L. 1758) fed on artificial diets. Aquaculture 8:115–128.

Ford, R.F. 1965. Distribution, population dynamics and behavior of a bothid flatfish, *Citharichthys stigmaeus.* Ph.D. Dissertation, University of California, San Diego. 243 p.

Frey, H.W., ed. 1971. California's living marine resources and their utilization. Calif. Dept. Fish and Game. 148 p.

Gadomski, D.M., S.M. Caddell, L.R. Abbott, and T.C. Caro. 1990. Growth and development of larval and juvenile California halibut, *Paralichthys californicus*, reared in the laboratory. Pages 85–98 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Haaker, P.L. 1975. The biology of the California halibut, *Paralichthys californicus* (Ayers) in Anaheim Bay. Pages 137–151 *in* D.E. Lane and C.W. Hill, eds. The Marine Resources of Anaheim Bay. Calif. Dept. Fish and Game, Fish Bull. 165.

Hammann, M.G. and A.A. Ramirez-Gonzalez. 1990. California halibut, *Paralichthys californicus*, in Todos Santos Bay, Baja California, Mexico. Pages 127–144 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Helvey, M. and J.F. Witzig. 1990. An analysis of the California halibut, *Paralichthys californicus*, recreational fishery, 1980–1987. Pages 359–372 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fishery Bulletin, U.S. 81:898–903.

Hulbrock, R. 1974. Lengths, weights and ages of 13 southern California marine gamefish. Calif. Dept. Fish and Game. 32 p.

Innis, D.B. 1990. Juvenile California halibut, *Paralichthys californicus*, growth in relation to thermal effluent. Pages 153–165 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Karpov, K. A. 1981. California halibut fishery, an evaluation of trawl ground legislation. Calif. Dept. Fish and Game, Mar. Resour. 29 p. Unpublished. Available from CDFG, Long Beach.

Kaupp, S.E. 1989. Growth and metabolic rate as a function of temperature in larval and juvenile halibut. Presented at: Symposium on the California halibut (*Paralichthys californicus*). Cabrillo Marine Museum, San Pedro, CA. May 23 & 24, 1989.

Kramer, S.H. 1990. Distribution and abundance of juvenile California halibut, *Paralichthys californicus*, in shallow waters of San Diego County. Pages 99–126 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resources and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Kramer, S.H. and J.R. Hunter. 1987. Southern California wetland/shallow water habitat investigations: annual report, 1987. NOAA/NMFS, Southwest Fisheries Center.

Kramer, S.H. and J.R. Hunter. 1988. Southern California wetland/shallow water habitat investigations: annual report, 1988. NOAA/NMFS, Southwest Fisheries Center.

Kuhlmann, D., G. Quantz, and U. Witt. 1981. Rearing of turbot larvae (*Scophthalmus maximus* L.) on cultured food organisms and postmetasmorphosis growth on natural and artificial food. Aquaculture 23:183–196.

Lavenburg, R.J. 1987. Report: reproductive biology of California halibut. Southern California Sportfish Assessment Program. Calif. Dept. Fish and Game.

Leitritz, E. and R.C. Lewis. 1976. Trout and salmon culture (hatchery methods). Calif. Dept. Fish and Game, Fish Bull. 164. 197 p.

Methot, R.D., Jr. 1983. Management of California's nearshore fisheries. Sport Fishing Institute. Mar. Rec. Fish. 8:161–172.

Myhre, R.J. 1967. Mortality estimates from tagging experiments on Pacific halibut. Rep. International Pacific Halibut Comm. 42. 43 p.

Oliphant, M.S. 1990. Historical catches of California halibut, *Paralichthys californicus*, by the commercial passenger fishing vessel fleet and recent (1980–1987) boat catch analysis. Pages 373–381 *in* C.W. Haugen, ed. The California halibut, *Paralichthys californicus*, resource and fisheries. Calif. Dept. Fish and Game, Fish Bull. 174.

Pauly, D. 1979. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Explor. Mer. 39:175–192.

Plummer, K. M., E. E. DeMartini, and D. A. Roberts. 1983. The feeding habits of juvenile-small adult California halibut (*Paralichthys californicus*) in coastal waters off northern San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 24:194–201.

Poxton, M.G. and S.B. Allouse. 1982. Water quality for marine fisheries. Aquaculture Engineering 1:153–191.

Reed, R. J. and A. D. MacCall. 1988. Changing the size limit: how would it affect California halibut fisheries. Calif. Coop. Oceanic Fish. Invest. Rep. 29:158–166.

Schmidt-Nielsen, K. 1979. Animal physiology: adaptation and environment, 2nd ed. Cambridge Univ. Press, Cambridge, England. 560 p.

Stephens, J. S., Jr., R. J. Lavenberg, and D. M. Gadomski. 1988. Continued investigations on the artificial propagation of the California halibut, *Paralichthys californicus*. Annual Progress Report for October 1987–October 1988. OREHAP Project. Mimeo. 25 p.

Townsend, C. R. and P. Calow. 1981. Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Inc., Sunderland, Massachusetts. 393 p.

Vetter, E. P. 1988. Estimate of natural mortality in fish stocks: a review. Fish. Bull., U. S. 86:25–43.

APPENDIX A

Variable	Description
L_t	length at time t
W_t	weight at time t
δ_w	$W_{t+1} - W_t$ = weight gain per fish per time step
N_t	number of fish at time t
F_t	weight of food required per fish per time step
O_{2t}	oxygen requirement per fish at time t
NH_{3t}	ammonia produced in time step t
H_2O_t	total water required per fish in time step t
O_{2d}	deficit in grams of dissolved oxygen per fish
T_t	number of tanks required at time t Cft cost for food in time step t
C_{et}	cost for electricity in time step t CH2Otcost for inflow water in time step t
C_{At}	total cost to culture to age t
t_L	time from stocking to recruitment
m_L	average mortality rate for fish from release to recruitment
S_L	average survival rate for fish from release to recruitment
C_{rt}	cost per fish stocked at time t that reaches recruitment
S_t	portion surviving from recruitment
C_r	catch per recruit, the fraction of recruited, stocked fish caught
Y_r	yield per recruit
P_f	culture cost per fish caught
B_r	net benefit = value of yield per recruit - cost per recruit

APPENDIX B

The computer programs used in both the cost estimates and the sensitivity analysis have been developed for distribution and can be obtained by writing the authors. The programs are written in TURBO Pascal to run on IBM-compatible personal computers. The programs make use of a graphics package that is specific to the graphics system on the computer. Information on the graphics environment, in which the programs will be run, should be included with the request.

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Horizontal and Vertical Movements of Pacific Blue Marlin Captured and Released Using Sportfishing Gear*

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Despite the commercial and recreational importance of Pacific blue marlin *Makaira nigricans*, little is known about their biology or behavior. This is due mainly to their large size and pelagic habitat and the difficulty in maintaining them in captivity or observing their behavior in the wild. However, two techniques are available to elucidate their movements: capturing and releasing marlin fitted with identification tags, and tracking of fish carrying ultrasonic transmitters.

The recovery of tagged marlin has enhanced our understanding of the long-term geographical range of individual fish and their minimum rates of travel (Squire 1974, Squire and Nielsen 1983, Bayliff and Holland 1986), and growing interest in the tag and release of marlin by sportfishermen should produce an increasingly precise picture of marlin movements. However, this technique cannot answer questions regarding the vertical movements of marlin, and questions remain concerning both the survival of tagged fish following the trauma of capture and the nature of their behavior immediately upon release.

Fine-scale observations of the horizontal and vertical movements of pelagic fish can be obtained for periods of up to a few days by tracking fish equipped with depth-sensitive ultrasonic transmitters (Holland et al. 1985, 1990; Bayliff and Holland 1986). For billfishes, this technique has been used to track swordfish *Xiphius gladius* (Carey and Robison 1981) and striped marlin *Tetrapturus audax* (Holts and Bedford In press). Similarly, Yuen et al. (1974) tracked Pacific blue marlin but used temperature-sensitive transmitters to monitor ambient water temperature from which depth was later calculated using bathythermograph data. However, this study heightened concerns about tagging mortality rates because three of the five tagged fish died soon after release.

Here we report on the movements of six Pacific blue marlin tracked in the waters around the Hawaiian Islands. Of particular interest were survivorship and behavior of the fish immediately upon release, their patterns of vertical movement, and their overall patterns of horizontal movement. To discern any common patterns of movement associated with one particular area of ocean, three fish were caught and tracked from one well-defined location on the Kona coast of Hawaii. For comparison, two other tracks were initiated several miles away along the same coast, and one marlin was tracked off the Waianae coast of Oahu.

Methods

The ultrasonic tracking techniques employed were identical to those used previously to track yellowfin tuna (Holland et al. 1985, 1990; Bayliff and Holland 1986). The transmitters used in the present study had a nominal life span of 3 days and a maximum working pressure of 500 psi (Vemco, Halifax County, Nova Scotia). The signal, encoding depth information by variable pulse interval, was recorded on audiotapes for later onshore plotting of vertical movements of the fish. Horizontal location was determined every 15 minutes (or more frequently when necessary) by using a combination of Loran-C, radar, visual, and bathymetric fixes. Water temperature was measured by expendable bathythermographs deployed approximately every 3 hours.

Aggregate depth and temperature distributions were calculated (with 10-m and 1°C bins, respectively) as percentages of the total track time spent at any particular depth or temperature. For temperature, the combined distributions of all fish were calculated as the percentage of time spent in the various temperature strata relative to the upper mixed layer.

Each transmitter was attached with a 10-cm length of 130-lb test monofilament to a stainless steel "arrowhead" (~2.75 × 1.75 × 0.1 cm; Fig. 1) modified from the type

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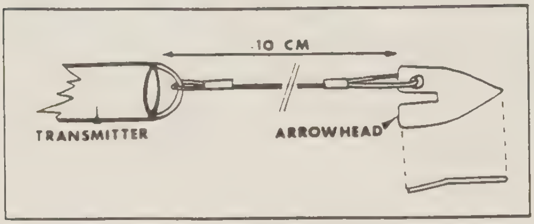

Figure 1
Tag attachment system for Pacific blue marlin. A stainless steel arrowhead, with downcurved tines and central notch to accommodate the prong of the applicator pole, is attached to the transmitter body with a 10-cm length of 130-lb test monofilament crimped in two places.

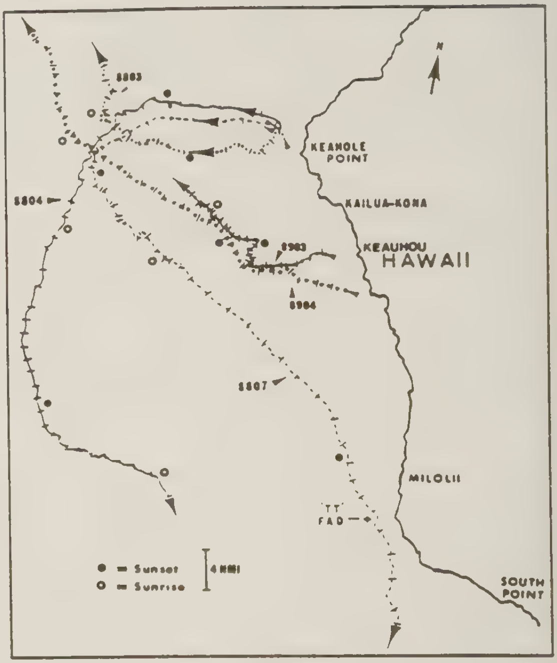

Figure 2
Horizontal movements of five Pacific blue marlin tagged off the Kona coast of Hawaii: three off Keahole Point and two off Keauhou. Lines perpendicular to the tracks represent hourly positions.

used by Yuen et al. (1974) and Carey and Robison (1981). The arrowhead fitted into the tip of a standard tagging pole to which the transmitter was loosely bound with rubber bands (Yuen et al. 1974, Holland and Bayliff 1986). The fish was harpooned in the trunk musculature, thereby allowing the transmitter to lie against the surface of the fish alongside the forward half of the dorsal fin. Once the transmitter was attached, the fish was released by cutting the leader, leaving the hook in place.

Fish were caught by surface trolling with artificial lures and standard sportfishing rods and reels. Two of the fish were caught on the tracking research vessel *Kaahele'ale*, and four were caught by teams participating in the 1988 and 1989 Hawaii International Billfish Tournaments (HIBT). In these latter cases, the transmitter and applicator pole were passed to the anglers' vessels during the fighting of the fish. Crew members then tagged the fish while the tracking vessel stood by ~100 m away. Once the fish had been released, tracking began.

To replicate tracks from one well-defined area, three tracks were initiated on the fishing grounds off Keahole Point, Hawaii. This is an area approximately 5 nautical miles (nmi) long and 2 nmi wide that is renowned for high catch rates of marlin during certain periods of the summer. For comparison, two other tracks were initiated from locations ~12 nmi south of the Keahole grounds, and one fish was tracked off Barbers Point, Oahu.

Results

Six Pacific blue marlin were tracked. The three Keahole fish were all caught within a 1-nmi radius over a span of 19 days in 1988; one track was 24 hours, and two were of 42 hours duration each (Fig. 2). In 1989, over a period of 4 days, two marlin were tracked from starting points ~4 nmi apart off Keauhou and were tracked for 26 and 29 hours (Fig. 2). The Barbers Point fish was tracked for 7 hours. Thus, all fish survived for at least 7 hours after release, and there is no reason to believe that any of the fish subsequently died as a result of the capture and tagging procedure.

Synopsis of tracks

Fish 8710 (weighing ~150 kg) was caught on a single-hooked artificial lure trolled behind the tracking vessel *Kaahele'ale* at a location 7 nmi west of Barbers Point, at 0904, 18 October 1987. After a fight time of 30 minutes, the fish was brought to the side of the boat. The fish was cleanly hooked through the bill and was immobile. The transmitter was embedded dorsolaterally, about a third of the way back along the dorsal fin. After release, the fish glided downwards and away from the boat and swam away on a southwesterly (offshore) course, which it maintained for the duration of the track. After 7 hours the fish was lost while at the surface. Data on the rate of horizontal movement for

Table 1

Rates of horizontal movement of captured and released Pacific blue marlin off Hawaii.

Track ID	Duration (hr)	Average speed (kn ± SD) Day	Night	Total	First hour
8710	7.0	1.21±0.27	NA	1.21±0.27	1.50
8803	24.0	1.48±0.31	1.37±0.32	1.43±0.30	1.20
8804	42.0	2.04±0.43	1.78±0.37	1.90±0.42	3.25
8807	42.0	2.25±0.67	2.09±0.67	2.18±0.65	3.25
8903	26.0	0.95±0.54	0.65±0.36	0.83±0.49	1.80
8904	29.0	1.62±0.37	1.68±0.39	1.65±0.37	3.00

this fish and the other five marlin are summarized in Table 1.

In terms of vertical behavior, this fish dove when released and spent the next 4 hours in the top 3 or 4 degrees of the thermocline at depths varying between 50 and 70 m. The fish then moved closer to the surface, spending 92% of the last 3 hours of the track within the surface mixed layer, moving between the surface and 35 m.

Fish 8803 (60 kg) was caught and tagged 2 nmi off Keahole Point at 1120, 8 August 1988, by a team participating in the HIBT. The fish was fought for ~20 minutes and described as tired but in good condition when released by the anglers. This marlin moved steadily west for ~12 hours before curving north during the night (Fig. 2). The fish was moving northwest when the track was terminated after 24 hours because of deteriorating sea conditions. The vertical movements of this fish (Fig. 3A) had a consistent "floor" where

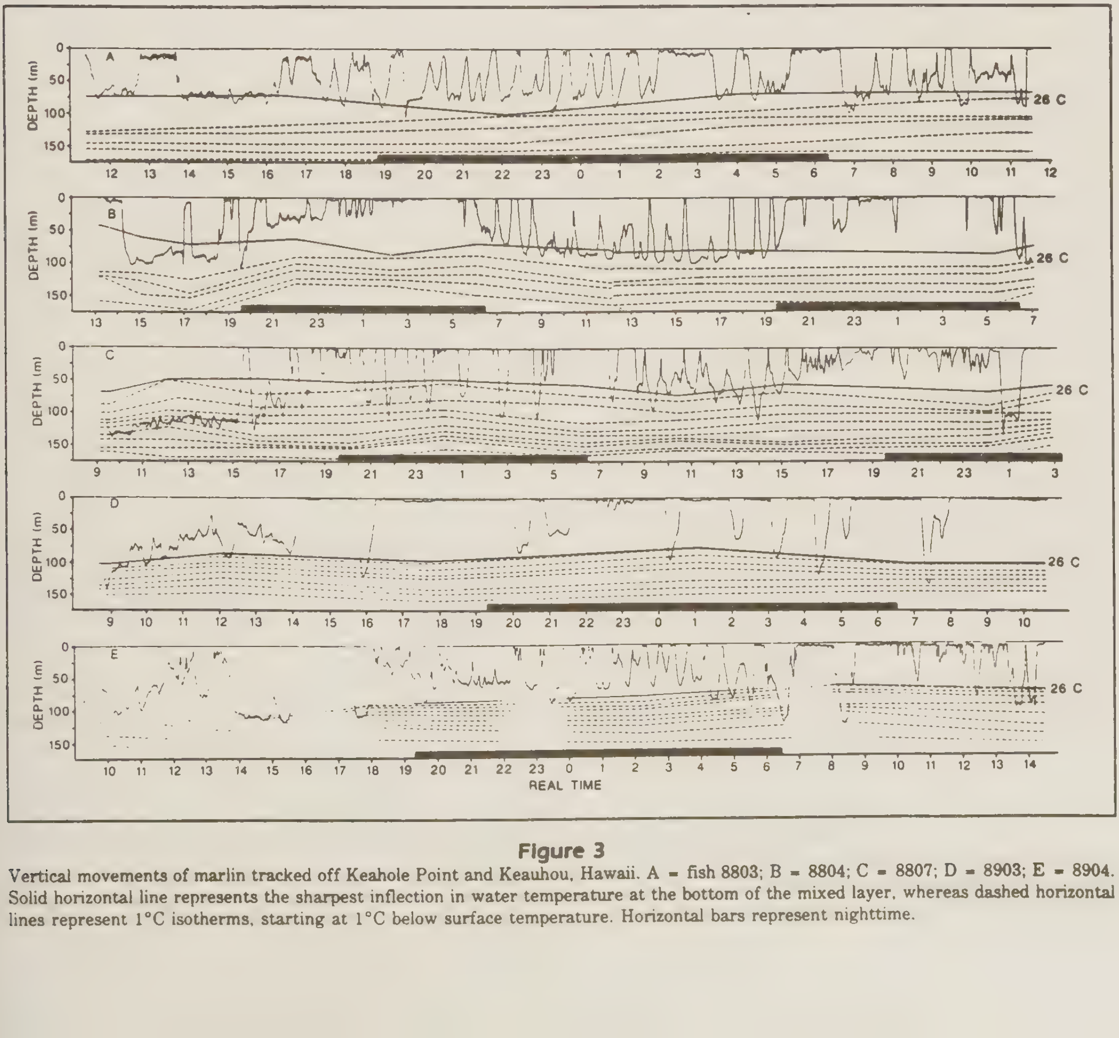

Figure 3

Vertical movements of marlin tracked off Keahole Point and Keauhou, Hawaii. A = fish 8803; B = 8804; C = 8807; D = 8903; E = 8904. Solid horizontal line represents the sharpest inflection in water temperature at the bottom of the mixed layer, whereas dashed horizontal lines represent 1°C isotherms, starting at 1°C below surface temperature. Horizontal bars represent nighttime.

the surface mixed layer met the top of the thermocline at depths varying between 75 and 100 m. During the daytime, the fish moved in and out of the top of the thermocline, with occasional excursions towards the surface; during the night, movements were more completely confined within the mixed layer with more time spent very close to the surface.

Fish 8804 (also estimated to weigh 60 kg) was caught and tagged by an HIBT team at 1310, 11 August 1988, 3 nmi off Keahole Point. Fight time and release condition were similar to fish 8803. After an initial, brief movement towards shore, this fish also proceeded directly west for about 8 hours before curving southward after sunset on the first night (Fig. 2). This direction was maintained all day during the second day until after sunset when it turned more shoreward. However, a southerly course was resumed after sunrise of the third day. The track was terminated after 42 hours.

The daytime vertical movements of this fish were focused around the interface between the mixed layer and the thermocline. From that depth (around 90 m) intermittent excursions were made to the surface. Nighttime distribution was shifted markedly towards the surface (Fig. 3B).

Fish 8807 was caught by the *Kaahele'ale* at 0900 on 27 August 1988, 3 nmi off Keahole Point. The fish, which was fought for 35 minutes, was caught using an artificial lure with a single hook that lodged in the base of the marlin's bill. The fish, weighing in excess of 160 kg, was completely immobile and floating belly-up at the side of the boat when the transmitter was attached near the midline in line with anterior insertion of the anal fin.

When the leader was cut, the fish sank slowly upside down under the boat but, after ~30 seconds, righted itself and began to swim slowly downwards. During the next hour, the fish traveled 3.25 nmi and, as with the previous two Keahole fish, headed steadily west, in this case for 7 hours. After sunset, the fish slowed and assumed a southeasterly course which it retained for the remainder of the track. After sunset on the second night, the fish returned close to the island and briefly visited fish aggregating device (FAD) TT off Milolii (Fig. 2). The fish was lost in rapidly deteriorating sea conditions off South Point, Hawaii, after 42 hours of tracking. At this time, the fish appeared to be continuing in a southerly direction.

Immediately upon release, this fish descended into the uppermost 2 or 3 degrees of the thermocline, where it remained for 6 hours as it swam steadily offshore. Upward excursions towards the surface started 3 hours before sunset, and movements on the second day were mostly in the thermocline-mixed layer interface with frequent upward movements, some of which reached the surface. As with the other Keahole marlin, nighttime distribution was shifted towards the surface, with considerable amounts of time spent at the surface (Fig. 3C).

Fish 8903, weighing ~75 kg, was caught and released 3 nmi off Keauhou Bay by a team in the 1989 HIBT. The fight time was ~20 minutes and the fish was lively when the transmitter was attached. Immediately upon release, the fish headed offshore for 5.5 hours before turning north (Fig. 2). This initial deviation in direction occurred ~11.5 nmi offshore and coincided with the marlin's first movement to the surface from the top of the thermocline, where it had been since the initial release (Fig. 3D).

Compared with other fish tracked in this study, this fish spent large amounts of time swimming slowly very close to the surface, often with the tips of its dorsal and caudal fins protruding above the surface. Although this "lazy" surface behavior is not uncommonly observed by fishermen, this was the only fish to demonstrate this behavior in the current study. The track was terminated after 24 hours, with the fish continuing to swim slowly at the surface in a northwesterly direction.

Fish 8904, also weighing ~75 kg, was caught and released by an HIBT team at a location ~2 nmi offshore of Kealakekua Bay, after a 36-minute fight. This fish also ran west (for ~6 hours) to a point 11.5 nmi offshore, at which time contact was lost for ~2 hours. When relocated, the fish had adopted a northwesterly course which it maintained for the remainder of the 29-hour track (Fig. 2). Vertical movements were similar to those of other fish, being largely constrained by the top of the thermocline and the surface, and averaging closer to the surface at night than during the day (Fig. 3E).

Temperature and depth distribution

Pooling the data from all six fish indicates that 82% of the daytime and 97% of nighttime distribution occurred in the mixed layer and top 2 degrees of the thermocline. In terms of depth, approximately 36% of the daytime and 60% of nighttime was spent between the surface and 30 m, the rest of the time being spent at greater depths (Fig. 4).

Discussion

Although the sample size reported here is quite small, these data represent a significant increase in the number of Pacific blue marlin tracked. Also, several aspects of the behavior of these marlin show remarkable consistency.

For instance, the behavior of all the fish tracked in this study was strongly influenced by the interface

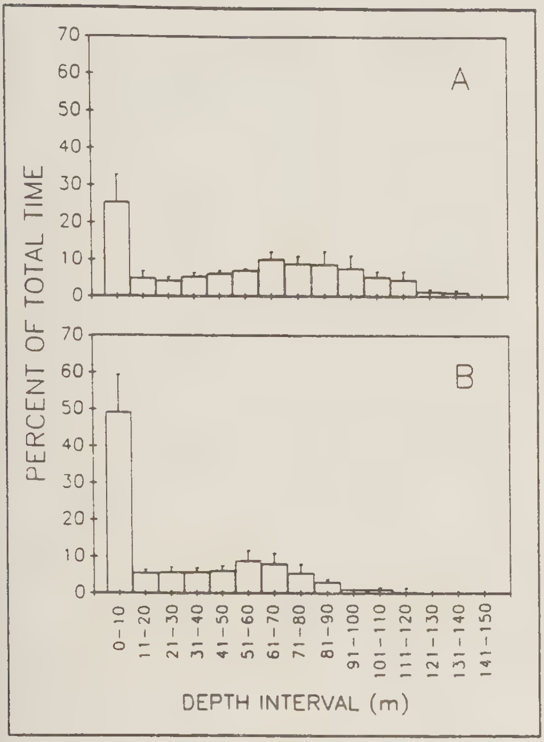

Figure 4

Aggregate depth distribution of six Pacific blue marlin off Hawaii during daytime (A) and nighttime (B).

between the surface mixed layer and the top few degrees of the thermocline, even though the depth of this interface varied between tracks. Unlike yellowfin tuna *Thunnus albacares*, which are also associated with this feature (Carey and Olson 1982, Yonemori 1982, Holland et al. In press), the marlin only rarely dove below the top of the thermocline. Thus, a major portion of the distribution of these marlin was bracketed by the surface and the bottom of the mixed layer. This behavior—not making deep dives, and spending most time in the mixed layer and upper thermocline—is similar to that of striped marlin tracked off California (Holts and Bedford In press), but differs greatly from that of swordfish which make frequent deep dives into cold water (Carey and Robison 1981). Compared with the striped marlin tracked off California, most of the blue marlin in Hawaii spent a relatively small amount of time very close to the surface. This may be due to the shallower depth of the thermocline off California (15–25 m) compared with Hawaii (35–90 m). With the exception of fish 8903, which spent an atypical amount of daytime very close to the surface, the marlin tracked in the present study moved closer to the surface at night. This differs from the striped marlin data, but is consistent with the behavior reported for skipjack tuna *Katsuwonus pelamis* (Yuen 1970), swordfish (Carey and Robison 1981), yellowfin tuna (Yonemori 1982, Holland et al. In press), and bigeye tuna *T. obesus* (Holland et al. In press).

Upon release, all six marlin dove into the upper layers of the thermocline and remained there for several hours. Onset of consistent upward excursions from the thermocline appeared to represent the end of the post-capture recovery period, usually between 4 to 6 hours. The recovery period was initiated by comparatively high-speed swimming, with four of the six fish travelling farther in the first hour following release than at any other time during the tracks. Because marlin are obligate ram-ventilators, these fish may be swimming fast enough to repay the anaerobic metabolic debt incurred during the fight, but not so fast as to acquire new debt. The fast speeds of the first hour are even more remarkable considering that at least two of the fish appeared to be completely exhausted when tagged and released. Holts and Bedford (In press) also report deeper than normal depths and heightened activity levels immediately upon the release of striped marlin.

With the exception of slow-moving fish 8903, the range of swimming speeds of individual fish in our study (1.2–2.18 kn) are similar to the blue marlin (1.2–1.9 kn) of Yuen et al. (1974). This is somewhat faster than the striped marlin speeds (0.75–1.45 kn) observed by Holts and Bedford (In press). In the present study, most of the fish swam slightly slower at night than during the day.

One of the most remarkable features of the current study is the consistent direction of movement displayed by the marlin in the first several hours of each track. Even though the three Keahole fish could have moved anywhere within a 240°-sector without running into land, all three swam along parallel westerly courses that took them directly offshore. Also, initial deviation from these parallel tracks occurred in the same general area ~12 nmi offshore. Similarly, both fish caught off Keauhou swam offshore for ~6 hours along almost identical paths, and both made their first major directional changes between 11 and 12 nmi offshore. This point in these two tracks was separated by only ~0.5 nmi, even though the release sites were over 4 nmi apart. The previously longest track of a Pacific blue marlin (22.5 hours; Yuen et al. 1974) was also initiated off Keauhou, and also commenced with a 7 nmi-movement offshore, as did the Barbers Point marlin tracked in the current study.

These results suggest that direct movement offshore may be a common response to the trauma associated with capture and release: The first major horizontal direction changes often coincide with changes in vertical behavior and may represent the end of the recovery period.

Previous blue marlin tracks, and those acquired in the present study, share the characteristic of essentially straight or slowly curving azimuths. This contrasts with the movements of nearshore tuna (Yuen 1970, Holland et al. In press) and swordfish (Carey and Robison 1981) which frequently display cyclical diel movements that bring the fish back to their starting points. If Pacific blue marlin have such a pattern in Hawaiian waters, the cycle time for this behavior is longer than any of the tracks so far obtained. At present, the impression is that these animals swim along straight or slightly curving courses as they move through the area.

It is difficult to explain the difference in tagging mortality between this study in which no fish died and the previous one in which three of the five blue marlin died (Yuen et al. 1974). Holts and Bedford (In press) also report that none of their 11 striped marlin died as a result of tagging trauma. Their results, and the results reported here, support the practice of releasing marlin caught on artificial lures by sportfishing techniques, even if the fish are apparently exhausted.

Acknowledgments

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Citations

Bayliff, W.H., and K.N. Holland
1986 Materials and methods for tagging tuna and billfishes, recovering the tags, and handling the recapture data. FAO Fish. Tech. Pap. 279, 36 p.

Carey, F.G., and R.J. Olson
1982 Sonic tracking experiments with tunas. ICCAT Collective Volume of Scientific Papers XVIII (2):458–466. Int. Comm. Conserv. Atl. Tunas, Madrid.

Carey, F.G., and B.H. Robison
1981 Daily patterns in the activities of the swordfish *Xiphias gladius*, observed by acoustic telemetry. Fish. Bull., U.S. 79:227–292.

Holland, K.N., R.W. Brill, S. Ferguson, R.K.C. Chang, and R. Yost
1985 A small vessel technique for tracking pelagic fish. Mar. Fish. Rev. 47(4):26–32.

Holland, K.N., R.W. Brill, and R.K.C. Chang
In press Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull., U.S. 88(3).

Holts, D., and D.W. Bedford
In press Activity patterns of striped marlin in the Southern California Bight. *In* Stroud, R. (ed.), Planning the future of billfishes: Research and management in the 90's and beyond. Part II: Contributed papers. National Coalition for Marine Conservation, Atlanta, GA.

Squire, J.L., Jr.
1974 Migration patterns of Istiophoridae in the Pacific Ocean as determined by cooperative tagging programs. *In* Shomura, R.S., and F. Williams (eds.), Proc., Int. Billfish Symp., Kailua-Kona, Hawaii, 9–12 Aug. 1972. Pt. 2, Review and contributed papers, p. 226–237. NOAA Tech. Rep. NMFS SSRF-675, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

Squire, J.L., Jr., and D.V. Nielsen
1983 Results of a tagging program to determine migration rates and patterns for black marlin, *Makaira indica*, in the southwest Pacific Ocean. NOAA Tech. Rep. NMFS SSRF-772, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 19 p.

Yonemori, T.
1982 Study of tuna behavior, particularly their swimming depths, by use of ultrasonic tags. Far Seas Fish. Res. Lab. (Shimizu) Newsletter 44:1–5. [Engl. Transl. No. 70, T. Otsu, 1982, 7 p. Avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822.]

Yuen, H.S.H.
1970 Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27:2071–2079.

Yuen, H.S.H., A.E. Dizon, and J.H. Uchiyama
1974 Notes on the tracking of the Pacific blue marlin *Makaira nigricans*. *In* Shomura, R.S., and F. Williams (eds.), Proc., Int Billfish Symp., Kailua-Kona, Hawaii, 19–12 Aug. 1972. Part 2. Review and contributed papers, p. 265–268. NOAA Tech. Rep. NMFS SSRF-675, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

9021

Horizontal and Vertical Movements of Yellowfin and Bigeye Tuna Associated with Fish Aggregating Devices*

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Abstract.–The horizontal and vertical movements of yellowfin tuna *Thunnus albacares* and bigeye tuna *T. obesus* captured near fish-aggregating devices (FADs) were determined using pressure-sensitive ultrasonic transmitters. The movements of these FAD-associated fish were compared with the tracks of yellowfin tuna not associated with FADs. Tracks from 11 yellowfin and 4 bigeye tuna were obtained; these included 23 complete 24-hour periods of observation. Whether associated with FADs or a 40-fathom (75-m) reef dropoff, most yellowfin and bigeye tunas exhibited similar diurnal patterns. The fish tended to remain tightly associated with FADs or the reef dropoff during the day, move away at night, and return the next morning. The maximum range of these nighttime excursions averaged approximately 5 nmi. These tunas apparently treated the FADs as outliers of the coastal topography. This may not be the same behavior that results in the association of these species with drifting objects such as logs. Tuna can learn FAD positions and navigate precisely between FADs that are at least 10 nmi apart. When not associated with FADs or the 40-fathom dropoff, yellowfin tuna oriented to the bottom of the mixed layer (50–90 m) in daytime, whereas the bigeye occupied depths between 190 and 250 m. The daytime distribution of bigeye tuna seemed to be influenced by the depth of the 15°C isotherm. Both species swam closer to the surface at night. Swimming strategies possibly associated with energy and thermoconservation were observed.

Tropical and subtropical pelagic fishes aggregate around natural, drifting debris such as logs and mats of algae. Man-made, anchored floating objects, known as fish aggregating devices (FADs), have also proven effective in attracting and holding commercially important pelagic species (Shomura and Matsumoto 1982, Matsumoto et al. 1981, Brock 1985). Species commonly found around FADs in Hawaii are yellowfin tuna *Thunnus albacares*, bigeye tuna *T. obesus*, skipjack tuna *Katsuwonus pelamis*, dolphin or mahimahi *Coryphaena hippurus*, and wahoo or ono *Acanthocybium solandri*. The first commercial FADs were deployed in the calm waters of the Philippines in the early 1970s to attract yellowfin tuna (Kihara 1981), and in 1977 experimental FADs designed for use in high-energy, deep-water environments were anchored around the Hawaiian islands (Matsumoto et al. 1981). Due to the success of these bouys in aggregating fish, FADs have come to play an important role in the commercial, subsistence, and recreational fisheries of all the tropical and sub-tropical oceans of the world.

Despite the widespread use of FADs, left unanswered are important questions concerning their range of influence, optimal placement, and impact on surrounding fish populations. The behavioral patterns that result in fish being associated with floating objects of any type are poorly understood and not widely agreed upon (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Fedoryako 1982). However, the underlying mechanisms of aggregation have generally been assumed to be the same for both free-floating phenomena such as logs, and anchored man-made objects such as FADs (Shomura and Matsumoto 1982). To better understand the behavior of tunas associated with FADs, the movements of yellowfin and bigeye tuna caught within 500 m of these devices were tracked using pressure-sensitive ultrasonic transmitters. The movements of these fish were compared with those of tunas that were not associated with FADs, but with the reef perimeter surrounding the islands. In Hawaii and elsewhere in the Pacific, yellowfin tuna can be found in the vicinity of the 40-fathom (75-m) isobath where the island topography abruptly descends into very deep water. In fact, the dropoff of the outer reef edge is often so steep that

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the horizontal distance between the 40-fathom and 100-fathom (187-m) isobaths is measured in tens of meters. To observe the behavior of non FAD-associated tuna, three yellowfin tuna were tracked that were caught on or near the 40-fathom isobath around Oahu, Hawaii.

The influence of FADs on the vertical movements of these species was investigated by comparing the depth distributions of the two species in on-FAD (within 500 m of a FAD) and off-FAD (beyond 500 m of a FAD) situations. The depth distributions were analyzed with respect to ambient ocean temperatures, as measured by expendable bathythermographs.

Methods

The horizontal and vertical movements of individual fish were monitored by pressure-sensitive, 50 KHz ultrasonic transmitters (Vemco, Halifax, Nova Scotia, Canada). Fish caught on the tracking vessel by trolling and pole-and-line techniques were fitted with transmitters by passing two nylon "tie-wraps" through the dorsal pterygiophores and trunk musculature adjacent to the second dorsal fin (Fig. 1). The fish were out of the water for approximately 1 minute during this procedure. The fish were then released and followed using a directional hydrophone mounted on the tracking boat. Whenever possible, a distance of approximately 200 m was maintained between the fish and the boat. Geographic position was determined every 15 minutes by a combination of Loran-C, radar, bathymetric, and visual fixes. These techniques evolved from pioneering work in tuna tracking by Yuen (1970), Laurs et al. (1977), Carey and Olson (1982), and Carey (1983). A summary of previous ultrasonic tracks of tuna has been compiled by Hunter et al. (1986). A detailed account of the methods used in the current study has been published previously (Holland et al. 1985, Bayliff and Holland 1986).

The transmitters were equipped with pressure sensors, which modulated the rate of pulse transmission in response to changes in water pressure (depth). Thus, vertical movements of the fish were determined by measuring the time between signal pulses. These pulses were recorded on audiocassettes for analysis ashore. Expendable bathythermographs deployed approximately every 3 hours provided ocean temperature profiles, which were superimposed on the vertical movement plots. Pooled time-at-depth and time-at-temperature histograms were constructed from all tracks combined, using 10-m and 1°C bins averaged every 10 minutes. The data were analyzed for daytime and nighttime depth distributions. Differences in the temperature and depth distributions for day-versus-night and on-FAD versus off-FAD were analysed by factorial analysis of variance (SAS General Linear Models Procedure, SAS 1985). Portions of tracks occurring on-FAD or near the reef dropoff were not included in these calculations. Thus, the depth histograms and overall averages are compiled from movements that were not constrained by bottom topography or influenced by the presence of floating objects.

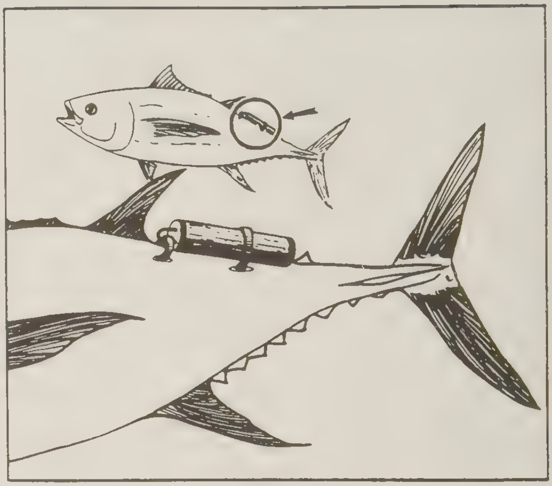

Figure 1
Transmitters were attached to yellowfin and bigeye tuna with two nylon straps inserted through the dorsal musculature and pterygiophores associated with the second dorsal fin (from Holland et al. 1985).

The tracking techniques used in this study are not capable of detecting small-scale changes in the horizontal swimming direction of the fish. Consequently, sustained swimming speeds have been calculated only from sections of tracks in which fish demonstrated prolonged straight-line movements. Swimming speeds were calculated as distance traveled per unit time and in terms of body lengths (fork length, FL) per second. Swimming speeds were calculated for each complete hour of "staight" running; these hourly rates were averaged to yield a sustained swimming speed for the relevant section of each track. Vertical movements were not included in these calculations.

Daytime and nighttime time-at-temperature histograms were generated for both yellowfin and bigeye tuna. Because of differences in absolute ocean-surface temperatures between different tracks, and because of

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previous indications that ocean thermoclines may be important orientation cues for tuna (Carey and Olson 1982), the time-at-temperature data were analyzed relative to the surface mixed layer. Thus, the mixed layer is referred to as ML, and the progressively colder 1°C isotherms as ML-1, ML-2, and so on.

Results

The results reported here are from tracks of 11 yellowfin and 4 bigeye tuna. Duration of tracks from release to track termination ranged from 5 hours to 6 days, with an average duration of 31.6 hours. Overall, these tracks encompass 23 complete 24 hour periods of observation. All 4 bigeye and 8 of the 11 yellowfin tuna were caught within 500 m of FADs. The remaining three yellowfin tuna tracks were from fish caught on or near the 40-fathom contour around the island of Oahu.

Horizontal movements

For yellowfin tuna, a clear pattern of horizontal movement was apparent. That is, during daylight the fish usually moved within a home range, staying in proximity to certain well-defined physical features, such as FADs or the outer reef dropoff. Eight of the 11 yellowfin tuna and 2 of the bigeye tuna showed aspects of this behavior, and this pattern was exhibited by both the FAD-associated and coastline-associated fish. Most of these fish made diurnal movements away from these daytime haunts, with the initial change in location often occurring around sunset.

FAD-associated yellowfin tuna These tuna spent daylight hours very close to the FADs, and then left those locations sometime between late afternoon and early nighttime to embark on extensive nighttime excursions, returning to the same or another FAD the following day. Five of the eight FAD-associated yellowfin tuna displayed aspects of this diurnal on-FAD and off-FAD behavior. A sixth FAD-associated fish showed signs of displaying this behavior, but was lost before this could be confirmed. The following is a brief synopsis of their horizontal movements.

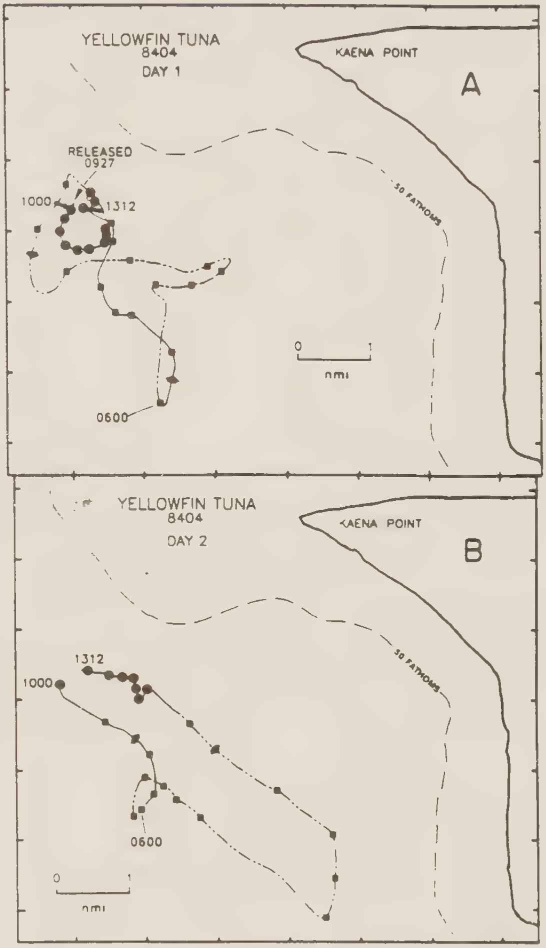

Figure 2

(A) 48-hour track of yellowfin tuna YF8404 tagged and released at 0927 at V FAD, Oahu. Circles = hourly marks when fish is on-FAD; squares = hourly marks when fish is off-FAD. In this and subsequent figures, solid line = daytime movements, dashed line = nighttime movements, and marks on figure axes = 1° divisions. On the first day (A) the fish remained very close to the FAD as it moved in a circular path in the current, departed the FAD after nightfall, and returned at 1312 the following day. The second day's behavior (B) was similar, despite a different pattern of movement by the FAD.

Yellowfin tuna YF8404 (51 cm FL) was caught and tagged at V FAD at 0927, and stayed within 100 m of the FAD for 11.3 hours before leaving it a few minutes after sunset (1925, Fig. 2A). The fish then made a nighttime excursion totaling 12 nmi before returning to within 100 m of the FAD by 1312 the next day. During the last few hours of this approach the fish moved very slowly, as if it was drifting in the prevailing current. Once at the FAD, the fish again stayed close to the buoy until departing at sunset on a second nighttime excursion of 11.25 nmi. The maximum distance away from the FAD was 3.0 nmi on the first night and 5.0 nmi on the second. On both excursions, the fish commenced moving back toward the FAD immediately after sunrise (Fig. 2A, B).

Two hours after fish YF8504 (47 cm FL) was tagged and released at S FAD at 0551, it made a 4-hour, 1-nmi excursion away from the buoy before taking up a posi-

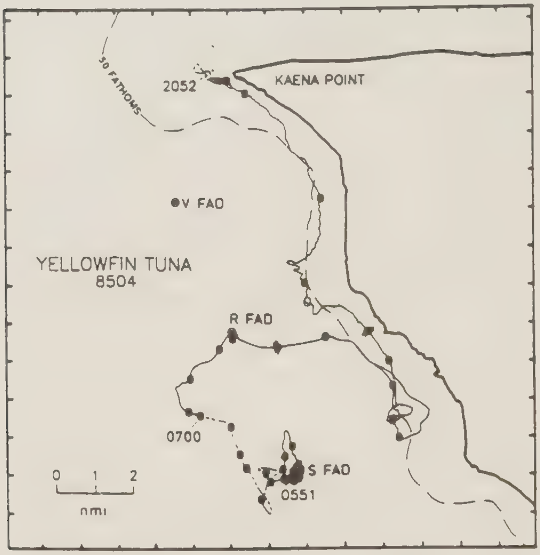

Figure 3
Yellowfin tuna YF8504 spent 8 daylight hours on the upcurrent side of S FAD before moving away at night. The next morning it moved to R FAD until disturbed by a school of porpoises, when it immediately took a direct course to the island dropoff, which it patroled for the rest of the day. In this and subsequent figures, squares = hourly position marks.

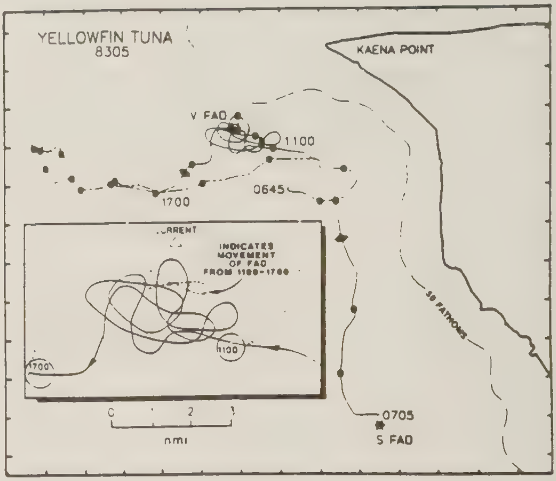

Figure 4
Yellowfin tuna YF8305 departed S FAD immediately after release at 0705 and took a direct course to the next nearest FAD, V (R was off station at the time), where it patroled almost exclusively in the upcurrent area (insert) before making an overnight excursion totaling 15 nmi.

tion within 50 m of the FAD for the remaining 8.0 hours of daylight (Fig. 3). During this time the fish was almost exclusively on the upcurrent side of the bouy. At 2345 the fish left the FAD and moved offshore; by sunrise the next day, it was 3.25 nmi from S FAD. The fish then moved 3.0 nmi in a direct course to the nearest adjacent FAD (R) arriving there at 0910. Once there, it stayed extremely close to the FAD and in the company of a school of other yellowfin tuna that could be seen from the surface. At 1020 a group of porpoises arrived and dove through the school of tuna, which appeared to scatter in all directions. The tagged fish dove and swam to the 40-fathom contour of the island, where it stayed for the rest of the day. Contact was lost just after sunset on the second night.

Fish YF8305 (55 cm FL), after being tagged and released at S FAD at 0705, swam for 4.0 hours on a direct course to V FAD, approximately 10 nmi away from the release point (Fig. 4). The fish spent 95% of the next 5.0 hours moving around on the upcurrent side of this FAD. In the late afternoon, the fish departed the FAD and spent most of the night farther offshore, moving in a 15-nmi loop before heading back toward V FAD the following morning. Just after first light, when the fish had returned to within 2 nmi of the FAD and appeared to be headed back even closer, the transmitter was shed.

The tracks of fish YF8406 (62.5 cm FL) and YF8501 (44.0 cm FL) were similar. During the daytime, both fish stayed very close to their respective FADs (for 9 and 12 hours, respectively), and both were lost at sunset in deteriorating sea conditions. Because there was no evidence of transmitter failure, and exhaustive searches at the FAD locations after dark failed to relocate the signal, it is reasonable to assume that both these fish were lost when they made sudden evening departures from the vicinity of their respective FADs.

Fish YF8302 (64 cm FL) was caught and tagged at S FAD, but lost 5.0 hours later. When contact was lost, the fish had departed the release site, but appeared to be curving back toward the bouy.

Fish YF8502 (74.5 cm FL) was similar to other FAD-associated yellowfin tuna in that, for the first 5.0 hours of the track (0600–1100), it stayed in close proximity (within 100 m) to S FAD. However, it then moved steadily away but was lost 12 nmi southwest of the buoy due to equipment failure after 13.5 hours of track and before any possible long-term trend had become apparent.

Fish YF8506 (75.25 cm FL) was caught near S FAD at 0630. Unlike the other FAD-associated yellowfin, it immediately began to move steadily away, maintaining a constant southwest course for the next 17.5 hours, at which time the track was terminated (Fig. 5).

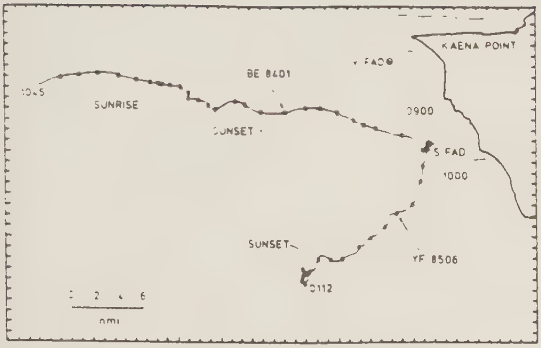

Figure 5
Bigeye BE8401 and yellowfin tuna YF8506 both departed S FAD almost immediately upon release and maintained quite straight azimuths at constant speeds. During darkness, both fish slowed down, and YF8506 became more variable in swimming direction.

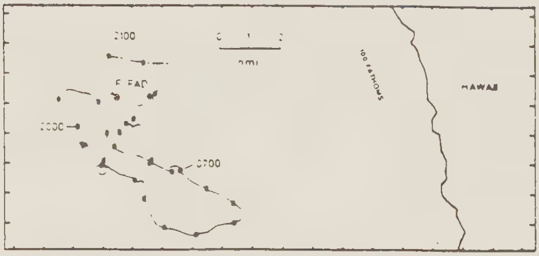

Figure 6
Caught and released after sunset at F FAD off the Kona coast of Hawaii, bigeye tuna BE8205 made a 24-nmi overnight loop before returning to the FAD by late afternoon of the following day.

FAD-associated bigeye tuna Four tracks were made of bigeye tuna caught near FADs. Of these four, one was lost after a few hours and before any diurnal patterns became apparent, one moved continuously away from the FAD (Fig. 5), and two displayed diurnal on-FAD and off-FAD behavior similar to that exhibited by the yellowfin tuna. The following is a synopsis of these two tracks.

Bigeye tuna BE8205 (74.5 cm FL) was caught and tagged 200 m from F FAD off Kona, Hawaii, about 1 hour after sunset (Fig. 6). Upon release, it proceeded on a 24.0-nmi overnight excursion which took it away from the FAD, before gradually reapproaching the FAD in the afternoon of the next day. The maximum distance it moved away from the FAD was 5.75 nmi. This track was then terminated after 24.0 h.

Fish BE8706 (72.0 cm FL) was caught at first light within 50 m of C FAD located off Kealakekua, Hawaii. The fish remained extremely close to the bouy throughout the day until 1 hour after sunset, when it made a 2-nmi excursion that lasted approximately 3 hours. The fish then returned to the immediate vicinity of the buoy, where it remained for the rest of the night and at least through noon of the following day, when the track was terminated after 30.0 hours.

Coastline-associated yellowfin tuna Three tracks were made of yellowfin tuna caught on the reef dropoff on the west coast of Oahu in water between 40 and 50 fathoms (75–95 m) deep. These fish were in the same size range as those caught around the FADs, and tracks spanning 6 days, 36 hours, and 37 hours were obtained, which encompassed a total of six day-night transitions. Two of the three fish displayed offshore excursions every night that they were tracked (a total of five nights). These tracks were as follows.

Fish YF8303 (70.0 cm FL) was caught and tagged at 0855 about 0.75 nmi off the leeward coast of Oahu on the 40-fathom dropoff (Fig. 7A). For the next 7 hours, the fish remained on or near the 40-fathom dropoff, before moving slightly further offshore in the late afternoon. During the subsequent 12 hours of darkness, the fish made a 17-nmi offshore excursion before returning to the 40-fathom contour in the second hour of daylight on the following day. The maximum distance away from the point at which it reencountered the dropoff was approximately 8.25 nmi. The fish remained on the reef slope for the remaining daylight hours until contact was lost at 1130, after 26 hours of tracking.

Forty-eight hours after contact was lost, a hydroacoustic search of the 40-fathom contour reestablished contact with the fish, and the track was resumed at 1426 of the third day (Fig. 7B). The fish spent the remaining daylight hours moving back and forth along the dropoff before moving offshore in late afternoon. The fish spent all night on a 13-nmi excursion before returning to the 40-fathom contour at first light on the next day. The greatest distance from the point of return to the dropoff was approximately 5.25 nmi. The track was suspended at 0730 on the fourth day. The fish was relocated on the 40-fathom isobath on the afternoon of the following (fifth) day at 1642 (Fig. 7C). Again, the fish moved offshore in the late afternoon and spent all night in deeper water on a 7.5 nmi excursion. Maximum distance from the point of return to the dropoff was 3.3 nmi. The time of arrival back at the 40-fathom contour was within 1 minute of the time of arrival on the previous day (Fig. 7B,C). The track was terminated at 0630 on the sixth day because of an impending storm. In summary, this fish was tracked over three day-night-day cycles spanning 6 days and, on each occasion, it made a nighttime off-

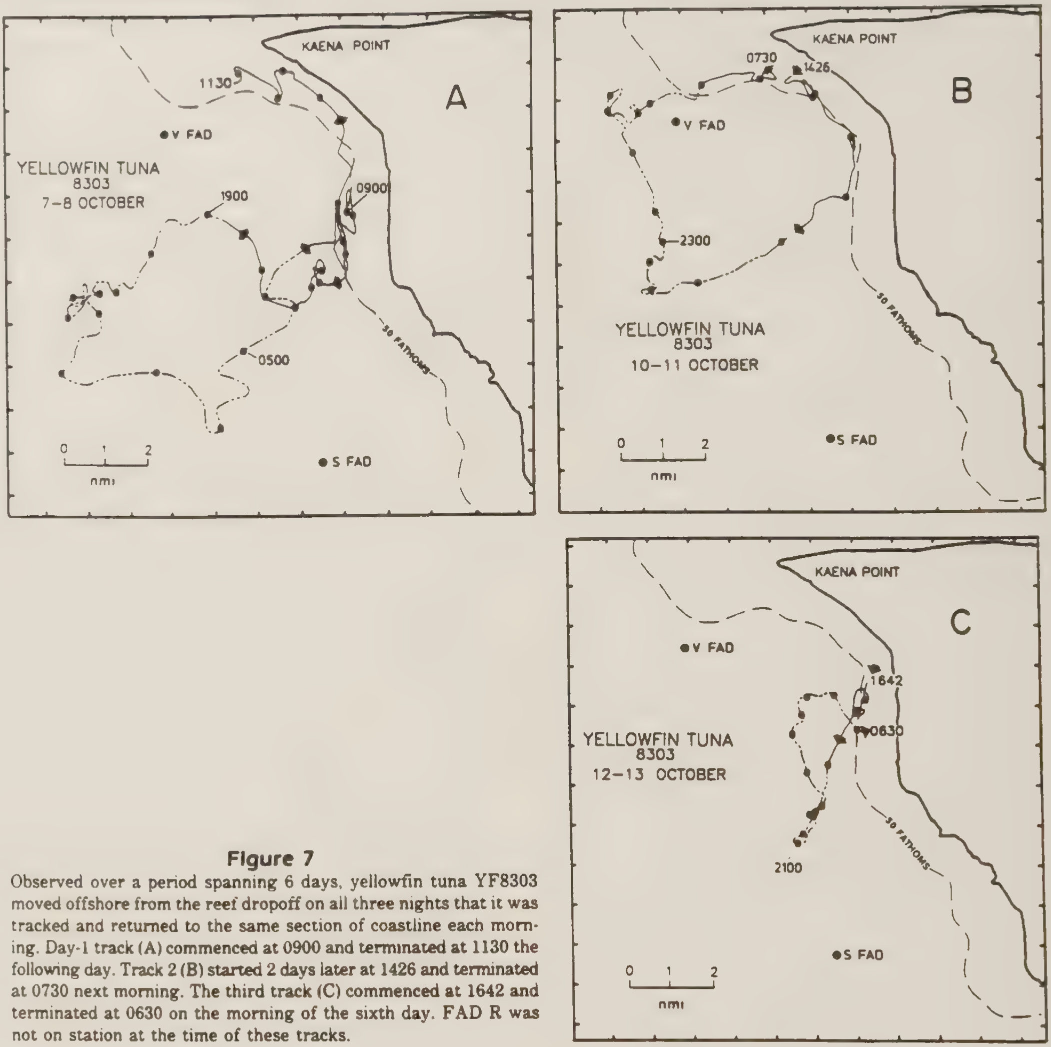
KAENA POINT
A
1130
V FAD
YELLOWFIN TUNA
8303
7–8 OCTOBER
1900
0900
0500
50 FATHOMS
S FAD
0 1 2
nmi
KAENA POINT
B
0730
1426
V FAD
2300
YELLOWFIN TUNA
8303
10–11 OCTOBER
50 FATHOMS
S FAD
0 1 2
nmi
KAENA POINT
C
V FAD
1642
0630
YELLOWFIN TUNA
8303
12–13 OCTOBER
50 FATHOMS
2100
S FAD
0 1 2
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Figure 7
Observed over a period spanning 6 days, yellowfin tuna YF8303 moved offshore from the reef dropoff on all three nights that it was tracked and returned to the same section of coastline each morning. Day-1 track (A) commenced at 0900 and terminated at 1130 the following day. Track 2 (B) started 2 days later at 1426 and terminated at 0730 next morning. The third track (C) commenced at 1642 and terminated at 0630 on the morning of the sixth day. FAD R was not on station at the time of these tracks.

shore excursion followed by a return to the 40-fathom contour on the following morning.

Fish YF8503 (47 cm FL) was caught on the 50-fathom contour at 1200 and stayed in this vicinity for 7.0 hours before moving offshore in the late afternoon to make a 24-nmi nighttime excursion (Fig. 8). The next morning, the fish returned to within 0.5 nmi of the section of coastline it had left the previous evening, the maximum distance from the point of return being 9 nmi. The tracking was temporarily suspended at 0930 and resumed at 1150, when the fish was relocated on the 40-fathom contour near Kaena Point. From here the fish embarked on a prolonged and constant run around the point and along the 40–50 fathom contour of the north shore of Oahu. At sunset of the second day, the fish again moved offshore. When contact was lost at 0100, the fish was 7.5 nmi offshore.

Fish YF8405 (57 cm FL) was caught on the 50-fathom contour and patroled this area for about the next 24 hours. This fish did not move offshore at night. Tracking was suspended at 0715 the second day, but resumed at 1715 the same evening when the fish was

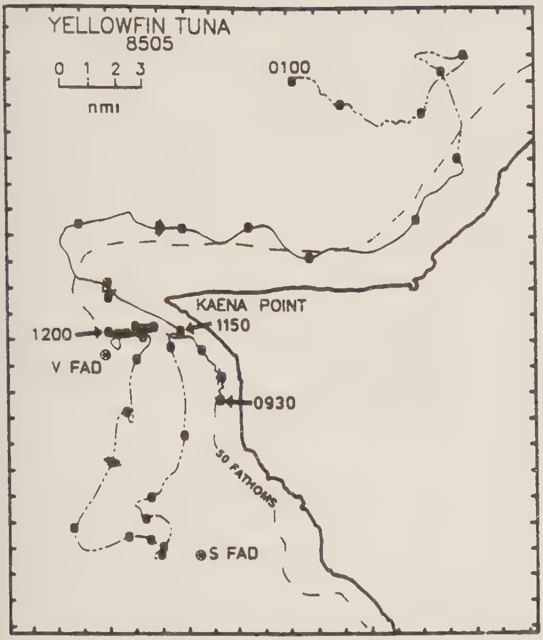

Figure 8
Yellowfin tuna YF8503 moved offshore and made a complete loop during the first night. Tracking was suspended between 0930 and 1150 of the second day. During the second day it swam at a constant pace along the reef dropoff bordering the north shore of Oahu before again heading offshore after sunset on the second night. This demonstrates that the diurnal onshore–offshore pattern is not site-specific to the west coast of Oahu. Contact was lost at 0100.

relocated on the 40-fathom contour. At times, the fish moved into water less than 30 m deep, but was lost just after sunset when the transmitter battery failed. However, this fish was caught two weeks later by a fisherman trolling at R FAD, 7 nmi away from the initial release point.

Combining the FAD-associated and coastline-associated fish, 7 of the 11 yellowfin tuna demonstrated diurnal behavioral patterns in which daytime haunts were abandoned at night. These 7 fish were observed to make a total of 11 nighttime departures from daytime locations. Of those 11 nighttime excursions, 7 were demonstrated to be completed loops wherein the fish returned to their original starting points. In addition, two FAD-associated bigeye tuna completed two nighttime-initiated loops. For the yellowfin tuna, the average maximum distance away from the following morning's destination was 5.28 nmi (SD = 1.9, N = 7). When the two documented bigeye tuna loops are included, the average maximum distance is 4.97 nmi (SD = 2.0, N = 9).

Swimming speeds Unlike the majority of the fish, one bigeye (BE8401) and one yellowfin tuna (YF8506) almost immediately departed their respective FADs and continued to swim away along straight azimuths for the entire duration of the tracks (Fig. 5). Consequently, large sections of these tracks were included in calculations of sustained swimming speeds. Daytime sustained swimming-speed data are summarized in Table 1.

The greatest distance traveled in 1 hour was exhibited at night by YF8503 which traveled 5.0 nmi. This is equivalent to 2.57 m (4.6 body lengths) per second (Fig. 8). When YF8504 was driven away from R FAD by a porpoise school, it swam the first half-hour towards the 40-fathom contour at a rate of 1.32 m (2.4 body lengths) per second (Fig. 3).

Table 1
Daytime sustained swimming speeds of selected yellowfin (YF) and bigeye (BE) tunas.

Track number	Fork length (cm)	Segment duration (h)	Average hourly speed (±SD)	
			m/s	Body lengths (FL)/s
YF8506	72.25	10.0	0.89 ± 0.15	1.19 ± 0.20
YF8502	74.50	7.0	0.95 ± 0.10	1.28 ± 0.14
YF8503	56.00	6.0	1.80 ± 0.38	3.20 ± 0.68
YF8305	54.50	4.0	1.32 ± 0.24	2.40 ± 0.40
		YF Mean =	1.24 ± 0.41	2.01 ± 0.96
BE8401	57.00	13.0	0.79 ± 0.20	1.38 ± 0.35
		Combined mean =	1.15 ± 0.41	1.89 ± 0.88

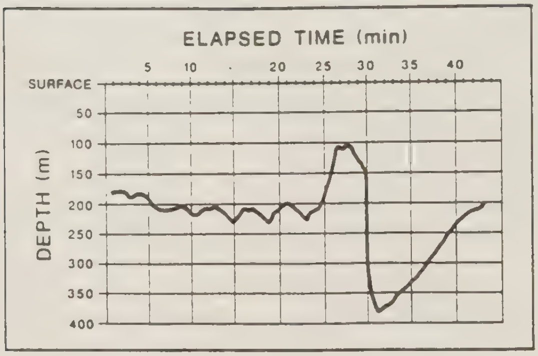

Figure 9
Fine-scale behavior of bigeye tuna BE8401 shown by 45-minute segment of vertical movements transcribed from data tape, including a rapid dive of 230 m in 1 minute, a rate equivalent to 6.7 body lengths/second. Ambient temperature at the maximum depth of 380 m was 9°C.

Vertical movements

The tape recordings of the pulsed signal from the transmitters resulted in detailed, continuous plots of vertical position. Rapid and small-scale changes in depth were discernible (e.g., Fig. 9), as were longer-term diurnal shifts in vertical distribution.

Day-night depth distributions In general, yellowfin tuna swam closer to the surface during darkness. For example, a dramatic change in the depth of swimming of fish YF8305 occurred exactly at sunset and lasted until first light the following morning, when it again began to swim deeper (Fig. 10). Combining all the offshore and off-FAD portions of the yellowfin tuna tracks yielded an average daytime depth of 71.3 m (±42.0 SD, $N = 333$), whereas the average nighttime depth was 47.3 m (±33.1 SD, $N = 444$). These daytime and nighttime depth distributions (Fig. 11A, B) are significantly different (ANOVA, $p = 0.0001$). However, this analysis also indicates significant variability among individual tracks.

Bigeye tuna swam at significantly greater daytime depths than the yellowfin tuna, and showed even greater shifts between daytime and nighttime distributions. When off-FAD, the predominant bigeye tuna daytime distribution was between 220 and 240 m, whereas the predominant nighttime depth was between 70 and 90 m (Fig. 12A, B).

On-FAD versus Off-FAD depth distributions Swimming depths of five yellowfin and one bigeye tuna that were on- and off-FAD during daytime hours support the proposition that FADs tend to bring the fish closer to the surface than they would normally be in other offshore parts of the ocean. These tracks were analyzed to determine if significant changes in depth distribution occurred when the fish were aggregated around the FADs, independant of diurnal influences. When on-FAD, three of the yellowfin tuna were closer to the surface than when off-FAD, one showed no change in depth, and one was deeper. Pooling these data for this subset of yellowfin tuna gave a mean on-FAD depth of 59.3 m (±30.7 SD, $N = 225$), which is significantly different from the mean off-FAD depth of 85.2 m (±52.0 SD, $N = 239$).

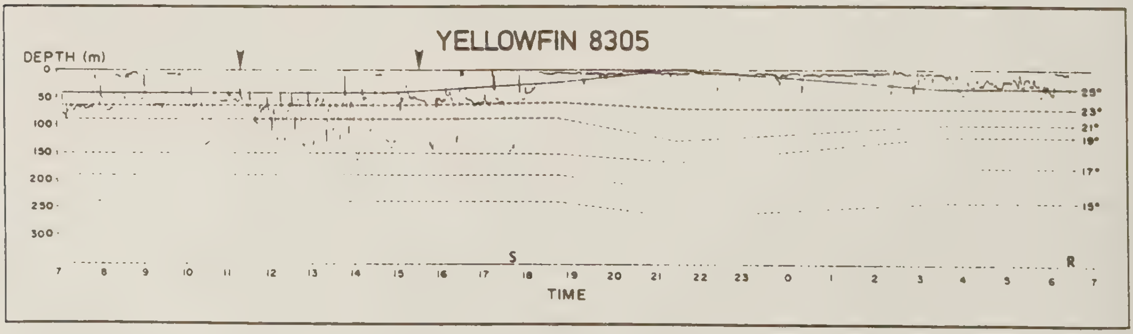

Figure 10
Plot (24-hour) of vertical movements of yellowfin tuna YF8305. In this and subsequent figures. S = sunset. R = sunrise. Arrows denote the beginning and end of time spent at V FAD. Before and after this period, the fish exhibited the "traveling" behavior of making abrupt shifts between the surface and the top layers of the thermocline. Once at the FAD, the vertical behavior became predominantly sinusoidal. All dives made both on- and off-FAD had a consistent floor around 20°C between 140 and 150 m. The rapidly descending trace at end of plot denotes the tag being shed from the fish.

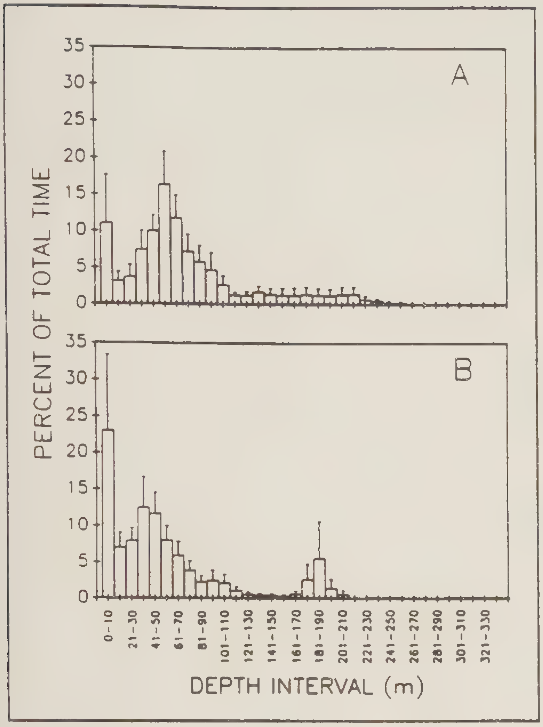

Figure 11
Yellowfin tuna daytime distribution (A) shows two modes, one at the surface and one between 60 and 90 m, which corresponds to the normal position of the interface between the mixed layer and the top layers of the thermocline. Nighttime distribution (B) reflects the tendency of these fish to swim closer to the surface at night. In this and subsequent histograms, bars = standard error.

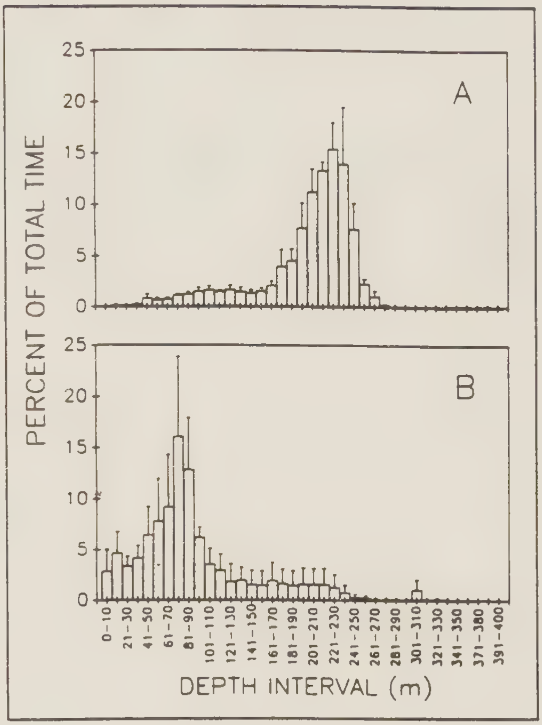

Figure 12
Daytime distribution of bigeye tuna (A) displays a major mode between 200 and 240 m, whereas nighttime distribution is much shallower (B), with the predominant distribution falling between 70 and 90 m.

The tendency of FADs to bring fish closer to the surface was even more apparent in the deeper-swimming bigeye tuna, as was dramatically demonstrated by BE8603 which stayed close to S FAD for 6 hours of daylight before moving away at midday. Figure 13 illustrates the rapid change of depth that coincided with

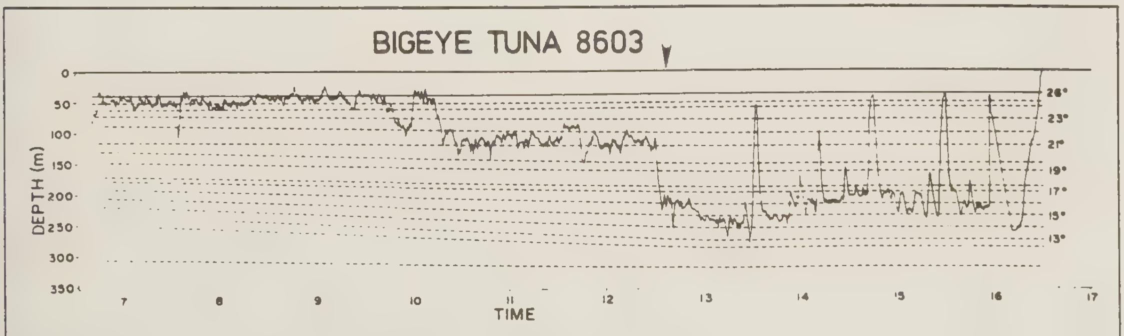

Figure 13
Plot of the on-FAD and off-FAD movements of bigeye tuna BE8603. Arrow indicates when fish departed R FAD.

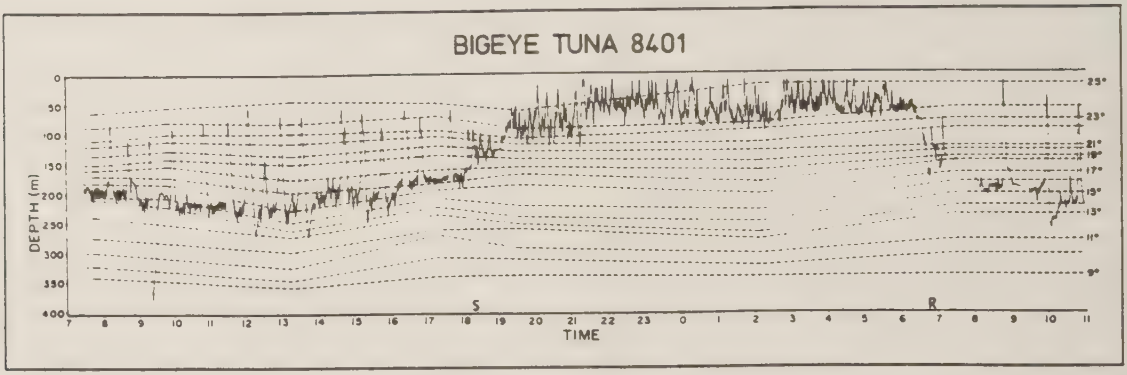

Figure 14
Plot of day-night-day movements of bigeye tuna BE8401. The rapid dive shown in Figure 9 can be seen at 0915 on the first day.

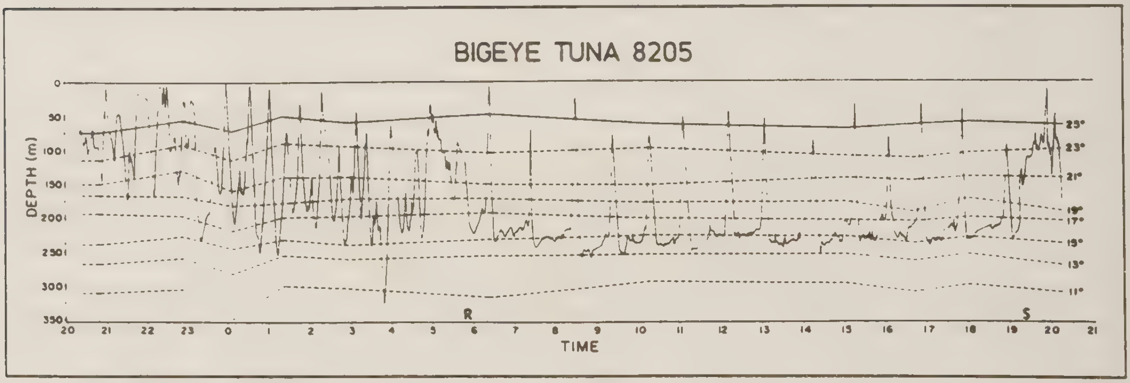

Figure 15
Plot of vertical movements of bigeye tuna BE8205 showing extremely regular daytime upward excursions. These excursions consistently terminated in the zone encompassing the interface between the mixed layer and the thermocline.

the departure of this fish from the FAD. The subsequent depth and pattern of swimming were similar to those shown by the other bigeye tuna that departed their respective FADs almost immediately upon release (Figs. 14, 15). Bigeye tuna BE8706, which remained within 200 m of S FAD for 27.0 hours of the 30.0-hour track, displayed a predominant on-FAD daytime depth of between 50 and 60 m, whereas the predominant, pooled, daytime off-FAD depth of the other three bigeye tuna was 230 m.

Temperature distribution

For the yellowfin tuna, the surface mixed layer (ML) and first degree of the thermocline (ML-1) accounted for 68% of daytime distribution (Fig. 16A). After sunset, the mixed layer alone represented over 62% of the distribution of this species, with the upper 2 degrees of the thermocline contributing an additional 26% of the yellowfin tuna's nighttime distribution (Fig. 16B). Obviously, the warmer nighttime distributions are reflective of the generally shallower depths occupied during the hours of darkness.

In the case of the bigeye tuna, daytime distribution was more dependent on absolute temperature than temperature relative to the surface mixed layer. Thus, in daytime 62.5% of the pooled off-FAD distribution occurred between 14° and 17°C (Fig. 17A). On an individual basis, the strong influence of temperature on daytime vertical distribution was demonstrated by fish BE8401 which consistently oscillated between the 15° and 17°C isotherms even though these isotherms were changing in depth over the course of the track (Fig. 14). Of this bigeye tuna's daytime movements, 68%

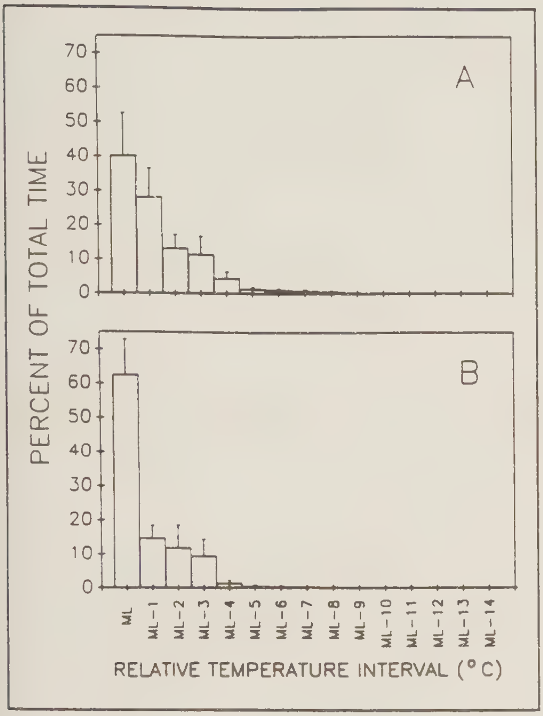

Figure 16
Yellowfin tuna temperature distributions relative to the upper mixed layer (ML). (A) day, (B) night.

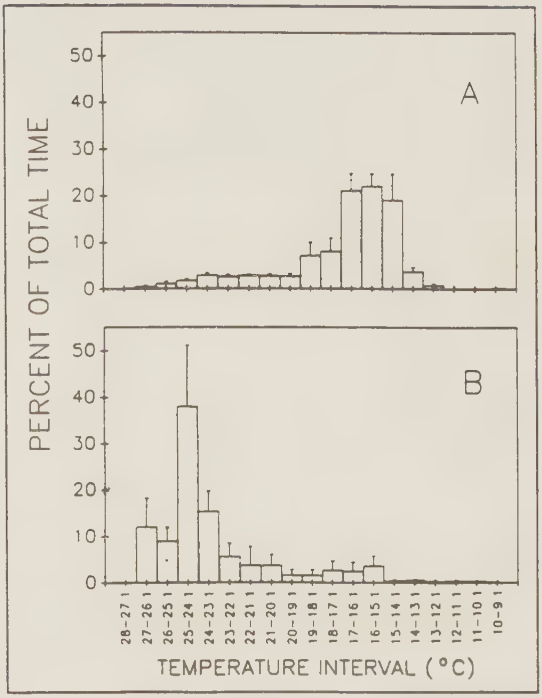

Figure 17
Bigeye tuna temperature distribution. (A) day, (B) night.

occurred between 14° and 17°C. Similarly, BE8205 spent 70% of daylight hours between the 14° and 16°C isotherms (Fig. 15), and BE8603 spent 76% of off-FAD daylight hours between 14° and 17°C isotherms (Fig. 13).

As with the yellowfin, bigeye tuna occupied warmer waters at night (Fig. 17B). The difference between daytime and nighttime temperature distributions was greater for bigeye than for yellowfin tuna because of the much deeper and colder daytime distribution of the bigeye tuna and their comparatively large nocturnal upward shift.

Regular, large, upward excursions were a major feature of the daytime swimming behavior of all the bigeye tuna that were tracked in off-FAD situations (Figs. 13, 14, and 15). This behavior occurred regardless of the type of horizontal movement (e.g., meandering versus straight line). These excursions were comprised of rapid ascents and descents of uniform rate. Ascents usually peaked close to the bottom of the mixed layer and the descending phases usually terminated at the predominant daytime swimming depth. These regular excursions did not occur at night or when on-FAD. For example, these upward excursions were exhibited by fish BE8603 only after it departed S FAD and assumed a deeper off-FAD distribution (Fig. 13). The periodicity and duration of these large excursions were quite regular. For instance, 13 daytime peaks exhibited by BE8205 had a peak-to-peak interval of 57.7 minutes (±7.0 SD) and a duration of 12.0 minutes (±2.6 SD).

Individual fish of both species tended to adopt consistent upper and lower limits to their movements such that, even if they were making frequent upward and downward movements, these were often terminated at consistent depths or temperatures. The most common of these turnaround points was the zone encompassing the bottom of the surface mixed layer and the uppermost layers of the thermocline. Thus, in the case of yellowfin YF8305, the top of the thermocline represented the bottom of dives made from the surface and the starting and finishing points of dives made to deeper depths, most of which had a consistent "floor" around the 20°C isotherm at approximately 130 m (Fig. 10). Similarly, in addition to the well-defined temperature confines of their smaller vertical oscillations, most of the bigeye tunas' large upward excursions consistently terminated near the interface between the thermocline and the mixed layer (Figs. 13, 14, and 15).

Examples of possible fly-glide behavior (Weihs 1973, Carey and Olsen 1982) were observed in tracks of yellowfin and bigeye tuna, a very consistent example being BE8401, which exhibited "sawtooth" oscillations with a period of approximately 4 minutes and an amplitude between 35 and 45 m for the entire 11-hour daylight segment of the track. Similar, persistent oscillating daytime behavior was exhibited by fish YF8506 as it moved on a direct course away from S FAD (Fig. 18). For instance, between 0930 and 1815 this fish swam on a straight southwesterly course at an apparently constant horizontal speed of 1.02 m/second (Fig. 5). Assuming this constant speed, the descending angles during this period averaged 6.06° (±0.7 SD, $N = 11$), and the climbing angles averaged 9.55° (±1.4 SD, $N = 11$) with 100% of the climbing angles being greater than the descending angles. Also, of the measurable oscillations occurring between 0915 and 1815, 39 out of 46 (85%) displayed longer falling than rising phases, suggesting active upward swimming followed by a comparatively passive downward glide. These oscillations were characterized by constant rates of ascent and descent, with abrupt changes in direction linking the falling and rising phases (Fig. 18).

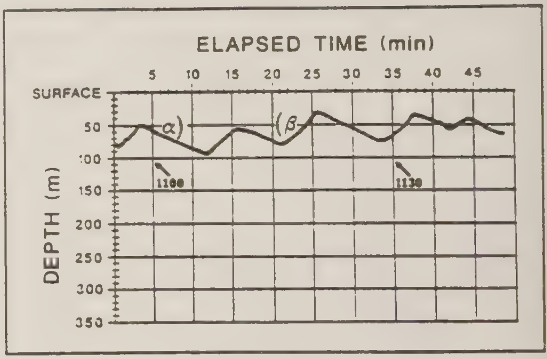

Figure 18

Yellowfin tuna YF8506 showed oscillations suggestive of "fly-glide" behavior while moving on an essentially straight course away from S FAD (cf. Fig. 5). All descending angles (α) were smaller than the climbing angles (β).

Discussion

Using two tie wraps appears to be a satisfactory way of attaching transmitters to tunas. Transmitters attached in this way were carried successfully by four captive fish for several weeks, and one of the tracked fish was caught in good health (and still carrying the transmitter) by a fisherman 2 weeks after we terminated the track. The similarity of vertical and horizontal movements across tracks also suggests minimal alteration of normal behavior.

The association of these tuna with a daytime range, whether FAD or reef perimeter, was extremely strong. In the case of FADs, several fish spent many hours within a few meters of the mooring line. Similarly, none of the reef-associated fish made significant offshore movements during daylight hours. In fact, the alongshore movements were remarkable for their fidelity to the outer reef contour. Combining FAD-associated and reef-perimeter fish, 10 of the 15 fish tracked in this study moved within a well-defined home range during daylight hours and two other fish were lost before any diel patterns could be observed. Most of the fish made nocturnal excursions away from their respective daytime habitats. Similar, consistent diurnal behavior has been previously observed in a 44-cm skipjack tuna, which returned to the same reef after making offshore excursions on each of six nights that it was tracked (Yuen 1970).

This skipjack tuna and the yellowfin tuna tracked in the present study represent the smaller size classes of these species. For fish of these sizes, the reef dropoff probably represents a zone of enhanced prey density where epipelagic species, such as bigeye scad *Decapturus crumenopthalmus*, mackerel scad *D. pinnulatus*, and flying fish (Exocidae), can be found in proximity to reef species which are also prey for these tunas (Hida 1973). The nighttime excursions away from the island reefs and FADs may be foraging behavior targeting on squid and shrimp, which come up from greater daytime depths and which are important components of yellowfin tuna diets (Reintjes and King 1953, King and Ikehara 1956, Brock 1985). Even though the reef-associated fish moved out into deeper water, the nighttime distribution of these yellowfin tuna was closer to the surface than their daytime depths.

The strong daytime association of yellowfin tuna with the FADs, and their nighttime excursions away from them, appears to be analogous to the behavior of island-associated fish patroling the outer reef dropoff. That is, yellowfin tuna appear to respond to FADs as outliers of the natural island topography (e.g., as offshore pinnacles). However, the FAD-associated fish may be paying an energetics penalty because the forage resource at FADs is probably considerably smaller than that available at the reef perimeter. This is indicated by the fact that yellowfin tuna caught at FAD locations have significantly smaller volumes of food in their guts and a significantly higher frequency of completely empty stomachs than do fish caught away from FADs (Brock

1985). Alternatively, it is possible that nighttime feeding excursions away from the FADs, combined with the apparently reduced daytime swimming activity at FADs as compared with nonFADs, result in an energetic savings equivalent to that of better-fed, but more active, open-ocean fish or reef-perimeter fish. Even though feeding may not occur as often at FADs as in other areas, FAD-associated tuna may conserve energy normally associated with active hunting. By orienting to FADs, the fish maintain a fixed position in the current flow and may feed on current-borne prey, a situation analogous to trout holding station in a river. The predominant upcurrent orientation of FAD-associated tunas may serve to intercept incoming prey items before they can use the FAD structure for shelter. These feeding advantages would not pertain to tuna associated with logs, which drift with the current and cannot provide the function of serving as a fixed point in a stream. Thus, although logs may indicate areas of enriched forage for planktivores by marking zones of Langmuir cell convergence (Fedoryako 1982), they are unlikely to supply the high food demands of even a medium-sized school of tuna, and, in fact, small fishes found in association with logs are not an important part of the diets of tuna taken from beneath logs (Hunter and Mitchell 1967).

There are other indications that different phenomena may underlie the association of tuna with natural debris and their association with FADs. For instance, fishing techniques which take advantage of log-associated tuna indicate that in these circumstances the tuna tend to aggregate around logs at night and move away in the daytime—exactly the opposite of the behavior observed in the current study. However, in the log situations, tuna behavior may be perturbed by the use of lights placed on the logs by fishermen. Also, since tunas probably are capable of magnetically mediated orientation (Walker 1984), and in our own study exhibited precise feats of navigation (e.g., returning to the same FAD, navigating between FADs, maintaining straight azimuths over prolonged periods of time), it is unlikely that tunas have trouble distinguishing between logs and FADs because, unlike logs, FADs are both stationary and attached to the ocean floor by visible (and possibly acoustically detectable) mooring lines.

The combined data yield an average nighttime excursion distance of approximately 5 nmi. This would indicate that to maximize the ability of FADs to aggregate yellowfin tuna consistently, and to minimize the influence of FADs on coastline-associated populations, FADs should be placed a minimum of 5 nmi from the nearest 40-fathom contour. This interpretation is supported by the track of fish YF8904 which rapidly traversed the 1.5 nmi to the 40-fathom contour when released at R FAD for a period of [illegible]. Similarly, YF8405 was caught at R FAD 2 weeks after being tracked along the adjacent coastline which, at its nearest point, is between 1.5 and 4.5 nmi away. In fact, optimal FAD placement would be greater than 15 nmi offshore or from the nearest 40-fathom contour so that the radii of influence of the FAD and the coastline do not overlap. Frequent anecdotal observations and the impressions of Hawaiian fishermen suggest that FADs located 15 nmi offshore are more consistently productive than FADs located closer to shore.

Daytime orientation of yellowfin tuna to the top layers of the thermocline, with excursions into the mixed layer and to the surface, and a nighttime shallowing into the mixed layer, are consistent with patterns observed by Yonemori (1982) and Carey and Olson (1982). The yellowfin tuna in the current study displayed a particularly strong adherence to the interface between the surface mixed layer and the thermocline when exhibiting straight-line movements. Similar behavior has been previously noted by Carey and Olson (1982). In the present study, these "traveling" fish would often abruptly alternate between the surface and the thermocline [illegible], both of which might serve to assist straight-line orientation [illegible] a truly three-dimensional nature. By contrast, fish orienting around FADs showed either little vertical movement or vertical movements that were sinusoidal and ranged within the mixed layer.

The depth and temperature distributions derived from the bigeye tuna tracks are in good agreement with distributional data obtained by analysis of longline fishing success (Saito 1975; Hanamoto 1974, 1987). These fishery data indicate maximum abundance at depths >200 m and in temperatures between 10° and 15°C, where the dissolved oxygen is >1 mL/L. However, the tracking data suggest daytime distribution (220–240 m, 14–17°C) is influenced at least as much by temperature as by depth, and none of the catch-rate studies indicate the dramatic nighttime upward shift that the tracking data reveal.

The average horizontal swimming speed derived from the straight sections of the current yellowfin tuna tracks was 4.36 km/hour (range [illegible] km/hour, Table 1), which is similar to the 4.27 km/hour average (range [illegible] km/hour) reported by Carey and Olson (1982) for fish having an average fork length 4.5× greater than those used in our study. This comparison would suggest that absolute traveling (sustainable) swimming speed for this species does not increase with size, at least for fish between 45 and 100 cm FL. This constancy of swimming speed, regardless of increasing fish length, is consistent with the model generated by Magnuson (1973, 1978), which predicts that increased weight associated with increasing length is offset in this species by the allometric growth of the swim bladder, thereby precluding the need to increase hydrodynamic lift through higher swimming speeds. However, the sustained swimming speeds observed during these tracks (average of 1.24 m/second) are considerably higher than the 0.5 to 0.6 m/second predicted by Magnuson (1978) for fish of this size. Obviously, field observations of larger fish would be useful in further testing the Magnuson model.

Periods of possible fly-glide behavior were observed in sections of tracks of yellowfin and bigeye tunas. These oscillations, which in one instance (YF8506) were exhibited for the entire daylight portion of a straight azimuth track, have been hypothesized to result in a saving of energy required for locomotion between two points (Weihs 1973, Magnuson 1978). As predicted by this model, most gliding phases lasted longer than the ascending phases, and the descending and ascending legs were connected by abrupt angles, which maximize energy transfer from the gliding to the flying phase. Thus, using the "fly" angle (β) of 9.55 and "glide" angle (α) of 6.06 obtained from YF8506, and a swim/glide drag ratio (k) of 1.2 (Magnuson 1978), the equation:

$$\text{Energy saving} = 1 - \frac{\tan\alpha}{\sin\beta + (\tan\alpha \cdot \cos\beta)} \times \left(1 + \frac{1 \sin\beta}{k \sin\alpha}\right)$$

results in an energy saving of 9.4% compared with level swimming over the same distance. And, where T is the increased time to travel the same distance using a fly/glide strategy as opposed to level swimming, using the equation

$$T = \frac{\sin\alpha + \sin\beta}{\sin(\alpha + \beta)}$$

indicates that this strategy results in only a 0.9% increase in time to travel the same distance.

The extremely regular, large, upward excursions made by all the off-FAD bigeye tuna during daylight hours may represent behavioral thermoregulation. At the low (14–17°C) ambient temperatures adopted by these fish, their core temperatures possibly drop below some threshold level which requires movement into warmer water to regain optimum body temperatures. If this is the case, it would suggest that there exists a strong motivation for inhabiting the deep cold layers observed during these tracks. A possible motivation would be the opportunity to feed on deepwater fish, squid, and crustaceans which the bigeye tuna then follow into shallower depths at night when these prey organisms migrate toward the surface. Monitoring the core muscle temperatures of bigeye tuna would indicate if, in fact, the large upward excursions are a form of behavioral thermoregulation which, when combined with physiological thermoconservation, allows these fish to exploit an otherwise unreachable resource.

Acknowledgments

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Citations

Bayliff, W.H., and K.N. Holland
1986 Materials and methods for tagging tuna and billfishes, recovering the tags, and handling the recapture data. FAO Fish. Tech. Pap. 279, 36 p.

Brock, R.E.
1985 Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregation devices, or can fish aggregation devices enhance local fish productivity? Bull. Mar. Sci. 37:40–49.

Carey, F.G.
1983 Experiments with free swimming fish. *In* Brewer, P.G. (ed.), Oceanography, the present and future, p. 58–68. Springer-Verlag, NY.

Carey, F.G., and R.J. Olson
1982 Sonic tracking experiments with tunas. ICCAT Collective Volume of Scientific Papers XVII. 2:458-466. Int. Comm. Conserv. Atl. Tuna, Spain.

Fedoryako, B.I.
1982 Langmuir circulation as a possible mechanism of formation of fish association around a floating object. Oceanology 22:228–232.

Gooding, R.M., and J.J. Magnuson
1967 Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486–497.

Hanamoto, E.
1976 The swimming layer of bigeye tuna. Bull. Jpn. Soc. Fish. Oceanogr. 29:41–44. [Engl. Transl. No. 21 by T. Otsu, 1977, 7 p.; avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.]
1987 Effect of oceanographic environment on bigeye tuna distribution. Bull. Jpn. Soc. Fish. Oceanogr. 51:203–216.

Hida, T.S.
1973 Food of tunas and dolphins (Pisces: Scombridae and Corphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri* (Engraulidae). Fish. Bull., U.S. 71:135–143.

Holland, K., R. Brill, S. Ferguson, R. Chang, and R. Yost
1985 A small vessel technique for tracking pelagic fish. Mar. Fish. Rev. 47(4):26–32.

Hunter, J.R., and C.T. Mitchell
1967 Field experiments on the attraction of fish to floating objects. J. Cons. Perm. Int. Explor. Mer 31:427–434.

Hunter, J.R., A.W. Argue, W.H. Bayliff, A.E. Dizon, A. Fonteneau, D. Goodman, and G.R. Seckel
1986 The dynamics of tuna movements: an evaluation of past and future research. FAO Fish. Tech. Pap. 277, 78 p.

Kihara, Y.
1981 Fishery based on the payao method in the Philippines. Suisan Sekai 30:78–84. [Engl. Transl. No. 76 by T. Otsu, 1982, 12 p.; avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.]

King, J.E., and I.I. Ikehara
1956 Comparative study of the food of bigeye and yellowfin tuna in the central Pacific. Fish. Bull., U.S. 57:61–85.

Laurs, R.M., H.S.H. Yuen, and J.H. Johnson
1977 Small scale movements of albacore, *Thunnus alalunga*, in relation to ocean features as indicated by ultrasonic tracking and oceanographic sampling. Fish. Bull., U.S. 75:347–355.

Magnuson, J.J.
1973 Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombroid and xiphoid fishes. Fish. Bull., U.S. 71:337–356.
1978 Locomotion by scombroid fishes: Hydromechanics, morphology, and behavior. *In* Hoar, H.S., and D.J. Randall (eds.), Fish physiology, vol. VII, p. 240–313. Academic Press, NY.

Matsumoto, W.M., T.K. Kazama, and D.C. Aasted
1981 Anchored fish aggregation devices in Hawaiian waters. Mar. Fish. Rev. 43(9):1–13.

Reintjes, J.W., and J.E. King
1953 Food of yellowfin tuna in the central Pacific. Fish. Bull., U.S. 54:91–110.

SAS
1985 SAS/STAT guide for personal computer, version 6 edition. SAS Institute Inc., Cary, NC.

Saito, S.
1975 On the depth of capture of bigeye tuna by further improved vertical longline in the tropical Pacific. Bull. Jpn. Soc. Sci. Fish. 41:831–841.

Shomura, R.S., and W.M. Matsumoto
1982 Structured flotsam as fish aggregation devices. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-22, Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., Honolulu, HI 96822, 9 p.

Walker, M.M.
1984 Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. J. Comp. Physiol. A 155:673–679.

Weihs, D.
1973 Mechanically efficient swimming techniques for fish with negative bouyancy. J. Mar. Res. 31:194–209.

Yonemori, T.
1982 Study of tuna behavior, particularly their swimming depths, by the use of sonic tags. Far Seas Fish. Res. Lab. (Shimizu) Newsletter 44:1–5. [Engl. Transl. No. 70 by T. Otsu, 1982, 7 p.; avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv. NOAA, Honolulu, HI 96822-2396.]

Yuen, H.S.H.
1970 Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27:2071–2079.

Monitoring Trends in Dolphin Abundance in the Eastern Tropical Pacific Using Research Vessels Over a Long Sampling Period: Analyses of 1986 Data, The First Year

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Abstract.– During 1986, the National Marine Fisheries Service began conducting long-term research vessel surveys to determine trends in population size of dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific. Line transect methodology was used by observers aboard two vessels for 120 days each. We assumed the variability associated with the abundance estimates would be relatively constant during the sampling period and investigated (1) annual changes in population size of the northern offshore spotted stock that could be detected within a 5-year (six survey) sampling period, and (2) the number of years required to detect a 10% annual decline with α and β error levels of 10%. The abundance estimate of the northern offshore spotted dolphin stock using the first year's data was 929,000 animals. After 5 years, a minimum 17.6% annual decline could be detected during which 62% of the stock would decrease. A 10% annual decline can be detected in a minimum of 8 years. Data from subsequent surveys will be investigated that may improve our ability to detect smaller annual declines.

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The National Marine Fisheries Service (NMFS) is responsible for assessing the status of dolphins taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) (Richey 1976). The status of spotted dolphins *Stenella attenuata* is of special concern because it is the major species taken by the fishery (Smith 1979). Of the three stocks of spotted dolphins, the northern offshore stock has been fished more frequently than any other stock. The four stocks of spinner dolphins *S. longirostris*, and the four stocks of common dolphin *Delphinus delphis*, are also taken. The four stocks of striped dolphin *S. coeruleoalba* and the Fraser's dolphin *Lagenodelphis hosei* are occasionally caught (Holt and Powers 1982). These five species are herein grouped and termed target species.

NMFS conducted assessments of target populations in 1976 (SWFC 1976) and again in 1979 (Smith 1979) using absolute stock abundance. The validity of the absolute estimates depended on several assumptions (i.e., all schools located directly on the trackline were detected, schools did not respond to the ship before being detected, etc.). Unfortunately, not all of these underlying assumptions were met (Holt and Cologne 1987, Holt 1987). Therefore, in 1984 Congress amended the Marine Mammal Protection Act and mandated that an alternative approach for assessing stocks be used that was less sensitive to biases. By using consecutive population estimates and establishing the first estimate as a base to which all subsequent estimates would be relative, we can detect trends in stock sizes over a long sampling period. These relative estimates can provide an assessment of stock condition if the biases in the abundance estimates are consistent over the sampling period.

In 1986, NMFS initiated a research program to monitor dolphin populations in the ETP which would utilize two research vessels for at least 5 years during which six surveys would be conducted. The research design (Holt et al. 1987) indicated that a 10% annual rate of decrease in northern offshore spotted dolphins could be detected (a total 41% decrease over six surveys). Herein, we present the population estimates for the first year's survey data. We also discuss effects of several factors on these base estimates, and, assuming data for subsequent surveys will have the same level of precision (coefficient of variation levels) as the first year, examine changes in population sizes that can be detected in 5 years or, conversely, the number of years required to detect various levels of change.

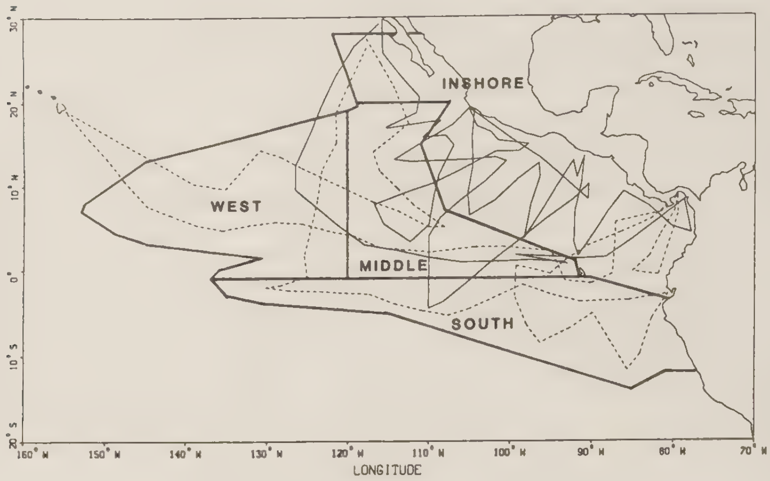

Figure 1
Tracklines traversed by the NOAA RV *David Starr Jordan* (solid) and *McArthur* (dash) during the 1986 dolphin survey, eastern tropical Pacific. Tracklines generated using noontime positions.

Materials and methods

Study area and survey coverage

The study area was described by Au et al. (1979) (Fig. 1). We partitioned the area into four strata: inshore, middle, and west located north of 1°S, and a south stratum. These strata were selected based upon preliminary examinations of historical distributions of dolphin stocks and oceanographic features.

The NOAA research vessels *David Starr Jordan* and *McArthur* traversed predetermined tracklines in the ETP during 29 July–5 December and 6 December, respectively (Fig. 1). Each vessel spent approximately 120 days at sea. Detailed operations, survey procedures and preliminary data summaries for each vessel are presented elsewhere (Holt and Sexton 1987, Holt and Jackson 1987).

On each ship, two observers used 25× binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. A third observer served as data recorder and searched directly ahead of the ship when not recording data. Two teams of three observers each alternately occupied the three duty stations. Each team was on duty for 2-hour shifts. During each shift, members spent approximately equal time occupying each duty station. Whenever possible, schools were approached and observers recorded independent "best" estimates of school size. If an observer could not obtain a best estimate, a "minimum" estimate was made. Independent estimates were averaged to obtain mean minimum and best estimates.

Abundance estimation

Estimates of population abundance of the target species (N_{ij}) are computed as (Holt and Powers 1982):

$$N_{ij} = \sum_{k=1}^{4} [D_k\, S_{tk}\, P_{tk}\, P_{ik}\, A_k/A_{ik}]\, [A_{ijk} + P'_{ij}\, A'_{ijk}],$$

where

D_k = estimate of density of all dolphin schools, both identified and unidentified to species, in area k,
S_{tk} = estimate of mean size of target schools in area k,
P_{tk} = estimate of proportion of dolphin schools which are target schools in area k,
P_{ik} = estimate of proportion of individuals of species i in target schools in area k,
P'_{ij} = estimate of proportion of individuals of stock j of species i in target schools in overlap region containing two stocks of species i (overlap region discussed in text),
A_k = total area inhabited by the target species in area k,
A_{ik} = area inhabited by species i in area k,
A_{ijk} = area inhabited by species i, stock j, in area k, and
A'_{ijk} = area inhabited by species i, stock j, in overlap region of area k.

The variance of N_{ij} was calculated using bootstrapped methods. For each stratum, the number of legs (segment of time during which all sighting conditions were consistent) of searching effort was tabulated, and then effort legs equal to that number were randomly selected with replacement. This effort and the associated sightings were used to calculate school density, school size, species proportions, and finally estimates of N_{ij}. This process was repeated 100 times. The bootstrapped variance of N_{ij} for each stock was calculated using these 100 estimates.

Formulae used to estimate school density are from Burnham et al. (1980), Holt (1985, 1987), and Hayes and Buckland (1983). The Fourier series (Crain et al. 1979) and hazard rate (Hayes and Buckland 1983, Buckland 1985) models both provided adequate fits to the perpendicular (sighting) distance data; however, the hazard rate model was used because, unlike the Fourier series model, it does not require subjective selection of the number of terms in the model and, therefore, could be used in the bootstrapped procedures. Of schools containing both target and non-target species, only the proportion of individuals of the target species was used in the school size estimates. Estimates of the proportion of all dolphin schools that were target schools (P_{tk}) were calculated using formulae from Holt and Powers (1982). Formulae to estimate the proportions (P_{ik}) of the number of individuals for each species of all target individuals are given by Barlow and Holt (1986).

All species of dolphins encountered in the study area were included in the density analyses. Estimates were calculated using only schools containing 15 or more animals. Smaller schools were not used because we believe small schools both on and off the ships' tracklines may be difficult to detect, especially during rough weather and may have been missed at a variable rate depending on prevailing weather conditions (Holt and Powers 1982).

Schools detected at increasing distances from the trackline tend to include disproportionately more large schools because there is a direct correlation between the size of a school and the probability of it being detected (Drummer 1985). This biases school size estimates upward and species proportions toward species which tend to occur in large schools. We attempted to adjust for this bias by weighting school size and species-proportion estimates by the inverse of the logarithm of school size (Holt and Powers 1982). Schools for which there were no "best" estimates of size were not used in the school-size or species-proportions calculations.

Because a 3.7 km (2.0 nm) truncation point provided the best fit of the hazard model to the data, only schools detected within 3.7 km perpendicular distance of the trackline were used to estimate school density. Schools detected greater than 3.7 km have little affect on the density estimates, and the perpendicular distance distributions of schools at greater distances were "spiked". These spikes are a result of the observers' tendency to round-off estimates of radial distances and sighting angles of schools detected at large distances from the vessel in multiples of 0.5 nm or 5°, respectively.

Some stocks of the same species have overlapping ranges (A'_{ijk}). These overlapping stocks include (1) coastal and northern spotted, (2) eastern and whitebelly spinner, and (3) Baja Neritic and northern common dolphins (Perrin et al. 1984). The relative number of dolphins of each overlapping stock (P'_{ij}) was calculated for data pooled over the range and, if applicable, over strata. The relative proportions of coastal and northern spotted, and of eastern and whitebelly spinner stocks, within their respective areas of overlap, were calculated as the average of their relative abundances (percent occurrence). Few data were available to determine relative proportions of the overlapping Baja Neritic and northern common dolphins. Therefore, population estimates for Baja Neritic were combined with northern common dolphins.

The area inhabited by each target species (A_{ik}) and each stock (A_{ijk}) used to calculate the population abundance estimates were those defined by Au et al. (1979) and Perrin et al. (1984). The size of each stratum (A_k) and the size of the area occupied by each stock in each stratum were calculated by counting the number of 1° quadrilateral squares in the stratum at each degree of latitude; partial squares were approximated. Next, the number of 1° squares was multiplied by the area in a 1° square for that latitude as described by Holt and Powers (1982).

Detecting trends in abundance

The variability associated with the population abundance estimates of northern offshore spotted dolphins during this first survey was examined to determine changes which may be detected from subsequent surveys using methods presented by Holt et al. (1987) and Gerrodette (1987). For Type I (α) and Type II (β) error levels of 0.10, we computed the number of years required to detect a minimum annual decrease of 0.10 and the minimum annual decrease in northern offshore spotted dolphins which could be detected at the end of the planned 5-year (6-survey) period. In addition, we calculated the total population decrease that would occur over the 5-year period given that annual level of decrease.

Results

During the entire survey, observers aboard both vessels searched 30,339 km and detected 1150 marine mammal schools. Dolphins were present in 749 of these

Table 1

Summary of 1986 dolphin survey in eastern tropical Pacific. Data were truncated at 3.7 km perpendicular distance. Schools with less than 15 animals were omitted from analyses. School sizes and species proportions weighted by inverse of logarithm of school size. Effort collected during sea states 0–5 were included in analyses. Data summed for both vessels. Total estimates calculated using effort summed over all four strata.

	Inshore	Middle	West	South	Total
Survey area (1000 km^2)	5,693	3,798	5,298	4,359	19,148
Percent of total survey area	30	20	28	22	100
Trackline searched (km)	11,889	7,846	3,877	4,056	27,669
Percent of searching effort	43	28	14	15	100
Dolphin schools					
Density (D_k) (schools/1000 km^2)	3.62	2.56	1.89	2.32	2.89
Number detected[1]	165	77	28	36	306
Mean target-species school size (S_{tk})	89.41	83.97	104.55	179.04	99.13
Number target schools[2]	126	71	25	27	249
Proportion target schools (P_{tk})	0.790	0.906	0.897	0.744	0.825
Proportion of target animals by species					
Spotted	0.239	0.378	0.347	0.170	0.266
Spinner	0.293	0.242	0.351	0.054	0.235
Common	0.296	0.108	0.008	0.661	0.305
Striped	0.163	0.272	0.126	0.056	0.160
Fraser's	0.009	0.000	0.168	0.059	0.035
Proportion of animals in overlap area					
Coastal spotted					0.395
Offshore spotted					0.605
Eastern spinner					0.703
Whitebelly spinner					0.297
Number of schools in overlap area					
Spotted					29
Spinner					96

[1] Includes unidentified dolphin schools.

[2] Includes schools identified as target species but for which a best estimate of school size was not made.

schools. While searching in the study area (Fig. 1), observers on both vessels searched 27,669 km and detected 306 dolphin schools containing 15 or more animals located within 3.7 km perpendicular distance of the trackline during Beaufort sea states of 5 and less (Table 1). The amount of effort and schools detected varied among strata; 43% of the total trackline searched and 54% of all dolphin schools detected were in the inshore area.

Abundance estimation

The estimate of $f(0)$ for data in the total area (pooled) was 0.522. Density estimates (D_k) in the four strata, calculated using the pooled $f(0)$, ranged from 1.89 to 3.62 schools/1000 km^2 (Table 1). Estimates of mean school size (S_{tk}) of target species ranged from 83.97 to 179.04 animals (Table 1). The proportion of identified dolphin schools that included target species (P_{tk}) ranged from 0.744 to 0.906 among strata (Table 1).

The proportions of individuals of all target schools that were spotted dolphins (P_{ik}) in the four strata ranged from 0.170 to 0.378 (Table 1). The proportions of the other target species among strata also varied greatly. For example, the proportion of common dolphins ranged from 0.008 to 0.661 (Table 1). Only 29 spotted dolphin schools were detected in the overlap region of the coastal and offshore spotted stocks. The proportion (P'_{ij}) of these that were offshore spotted dolphins was 0.605 (Table 1). Of 96 spinner dolphin schools detected in the area of overlap of eastern and whitebelly spinner stocks, the proportion of these that were eastern spinner dolphin individuals was 0.703.

The areas inhabited by each stock (A_{ijk}) of each target species (A_{ik}) in each stratum (A_k), and the overlapping areas (A'_{ijk}) inhabited by (1) coastal and offshore spotted dolphins and (2) eastern and whitebelly spinner dolphins, are shown in Table 2.

Relatively, common dolphins were the most abundant species (Table 3). The estimate of 929,000 northern offshore spotted dolphins represented 78% of the estimate of all stocks of spotted dolphins. The coefficient of variation (CV) of the abundance of the northern offshore spotted dolphon stock, CV(N_{ij}), was 0.255. The

Table 2

Area inhabited (km^2) by each dolphin species/stock in inshore, middle, west, and south strata, and in total survey area, eastern tropical Pacific.

Dolphin species/stock	Inshore	Middle	West	South	Total area
Spotted					
Coastal, non-overlapping	113,660			8,557	122,217
Northern offshore, non-overlapping	4,073,493	3,788,767	4,016,325		11,878,585
Coastal and northern offshore, overlapping	909,279				909,279
Southern offshore, non-overlapping				3,175,138	3,175,138
Coastal and southern offshore, overlapping				68,455	68,455
Total	5,096,432	3,788,767	4,016,325	3,252,150	16,153,674
Spinner					
Costa Rican	248,366				248,366
Northern whitebelly, non-overlapping			1,806,239		1,806,239
Eastern and northern whitebelly, overlapping	4,762,844	3,401,601	2,889,195		11,053,640
Southern whitebelly, non-overlapping	9,825	346,337	47,898	2,543,829	2,947,889
Eastern and southern whitebelly, overlapping	190,322			751,964	942,286
Total	5,211,357	3,747,938	4,743,332	3,295,793	16,998,420
Common					
Northern tropical	1,477,237	477,581			1,954,818
Western central tropical	17,886	1,273,546	2,207,221		3,498,653
Eastern central tropical	3,502,375	420,581			3,922,956
Southern tropical	829,881	847,176		1,239,588	2,916,645
Total	5,827,379	3,018,884	2,207,221	1,239,588	12,293,072
Striped					
Northern tropical	1,104,177	681,546			1,785,723
Western central tropical			2,870,874		2,870,874
Eastern central tropical	3,549,019	1,066,116			4,615,135
Southern central tropical	510,371	1,658,074	514,537	3,792,278	6,475,260
Total	5,163,567	3,405,736	3,385,411	3,792,278	15,746,992
Fraser's*	5,211,357	3,747,938	4,743,332	3,295,793	16,998,420
All species/stocks	5,848,469	3,797,734	5,298,266	4,203,366	19,147,835

*Used total spinner dolphin area.

Table 3

Estimates of base population sizes (N_{ij}) (10^3 animals) by stock for target dolphin species in total survey area, eastern tropical Pacific. Estimates weighted by size of each stratum.

Dolphin species/stock	N_{ij}	SE(N_{ij})	CV(N_{ij})
Spotted			
Coastal	36.0	8.6	0.239
Northern offshore	929.0	236.5	0.255
Southern offshore	218.5	120.3	0.551
Total	1183.5	365.4	0.309
Spinner			
Costa Rican	20.9	6.1	0.292
Eastern	579.6	192.2	0.332
Northern whitebelly	333.1	127.5	0.383
Southern whitebelly	83.1	32.9	0.396
Total	1016.7	358.7	0.353
Common			
Northern tropical	124.9	39.7	0.318
West central tropical	42.5	22.2	0.522
East central tropical	277.3	85.6	0.309
Southern tropical	943.2	388.8	0.412
Total	1387.9	536.3	0.386
Striped			
Northern tropical	92.4	20.2	0.219
West central tropical	99.9	40.7	0.407
East central tropical	230.6	48.6	0.211
Southern tropical	212.3	62.4	0.294
Total	635.2	171.9	0.271
Fraser's	247.9	202.5	0.817
Total	4471.2	1634.8	0.366

abundance estimate for eastern spinner dolphins was 579,600 animals with a CV of 0.332.

Trends in abundance

Assuming the CV(N_{ij}) for subsequent surveys will be constant during the sampling period, and with α and β errors equal to 0.10, a 10% annual decrease in abundance of offshore spotted dolphins can be detected in a minimum of 8 years. After 5 years, and assuming the CV(N_{ij}) of 0.255 will remain constant, a minimum annual decline of 17.6% may be detected during which a 62% decrease of the offshore spotted stock would have occurred.

Discussion

A biased estimate may be acceptable to detect trends in population changes if the bias is constant among annual surveys and if it results in a more precise estimate. For example, the estimate of school density that was calculated by fitting a detection function to data pooled over all strata is biased upwards because searching effort was not allocated to strata uniformly but proportionately to historical estimates of density. The inshore stratum, which historically had the largest density (Holt et al 1987), received a greater proportion of the searching effort (43% of total effort) compared with its relative size (30% of total area). However, the pooled estimate is more precise than the stratified estimate, and the bias should be consistent during subsequent years.

Our estimate of target school size (99.13 animals, Table 1) was half the estimate from aerial data collected in 1979 (199.8 animals per school) (Holt 1985). Although school size may have declined between 1979 and 1986, our estimate is similar to a previous school size estimate that used data collected 1979–83 aboard research vessels (119.9 animals per school) (Holt 1985). In addition, we used only schools detected within 3.7 km perpendicular distance of the trackline, while the previous aerial and ship studies used schools detected within 11.1 km perpendicular distance (approximate distance to horizon from ship). Our estimate using the 11.1 km perpendicular distance was 111.97 animals per school. The previous estimates from airplanes and ships may have been biased upward because large schools are more likely detected at greater distances than are small ones.

The inverse log weighting factor used to adjust biases in the school-size and species proportion estimates caused by detecting disproportionately more large schools may have over- or undercompensated by an unknown degree. Recent work by Drummer (1985) investigating size biases may be utilized during comparisons of this data and subsequent years' data.

Estimates of the relative proportions (P'_{ijk}) of coastal and offshore spotted dolphins and of eastern and whitebelly spinner stocks in their respective areas of overlap were based on data pooled over all strata and included all schools occurring within 11.1 km (6 nm) perpendicular distance from the trackline; however, they were based on small sample sizes (29 spotted and 96 spinner schools). These estimates may change with collection of additional survey data. However, the proportion of eastern spinner dolphins to whitebelly spinner dolphins in their overlap area was 0.703 during 1986 (Table 1) and was 0.714 when all research vessel data collected from 1976–86 were combined (207 schools).

Our population abundance estimates are intended to serve as the baseline estimates for relative comparisons using data collected during subsequent surveys. When our estimates of northern offshore spotted dolphins are compared with previous estimates, ours are much smaller than those made for data collected through 1979 (2,775,000 animals) (Holt and Powers 1982) and for data collected through 1984 (2,533,300 animals) (Holt 1985). Both the latter absolute and our current base estimates may be biased because they share common data collection constraints—failure to detect all trackline schools—which bias the density estimates downward. The older estimates may also contain other biases which result in relatively higher values. For example, those estimates used a combination of data collected aboard airplanes, research vessels and tuna vessels, and survey coverage was pooled over several years, seasons, and areas. However, some variables used to calculate our estimates used small data sets that may have resulted in less precise results.

Because our population estimates are intended to serve as the baseline estimate for relative comparisons using data collected during subsequent surveys, consistent bias during the sampling period will not jeopardize the results. Therefore, several options will be reviewed in analyzing subsequent years' data which may reduce variability associated with the population estimates. Sample sizes to calculate school sizes and species proportions may be increased by utilizing all schools detected at perpendicular distances from the trackline out to the horizon. We will investigate spotted dolphin abundance estimates using only schools of spotted dolphins. A computerized binocular system (Holt and Sexton 1987) may yield more precise estimates of radial distance and sighting angles to dolphin schools, and we have incorporated use of a ship-based helicopter to obtain aerial photographs of dolphin schools to calibrate observer estimates of school size. Hopefully, some or all of these factors may reduce the CV(N_{ij}) levels to around 12%, as anticipated by Holt et al. (1987) in initial survey design.

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Citations

Au, D., W.L. Perryman, and W. Perrin
1979 Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Adm. Rep. LJ-79-43, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 59 p.

Barlow, J., and R.S. Holt
1986 Proportions of species of dolphins in the eastern tropical Pacific NOAA-TM-NMFS-SWFC-56, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 44 p.

Buckland, S.T.
1985 Perpendicular distance models for line transect sampling. Biometrics 41:177–195.

Burnham, K., D. Anderson, and J. Laake
1980 Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72, 202 p.

Crain, B., D. Burnham, D. Anderson, and J. Laake
1979 A Fourier series estimator of population density for line transect sampling. Utah State Univ. Press, Logan, 25 p.

Drummer, T.D.
1985 Size-bias in line transect sampling. Ph.D. Diss., Univ. Wyoming, Laramie, 143 p.

Gerrodette, T.
1987 A power analysis for detecting trends. Ecology 68: 1364–1372.

Hayes, R.J., and S.T. Buckland
1983 Radial distance models for the line transect method. Biometrics 39:29–42.

Holt, R.S.
1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Adm. Rep. LJ-85-20, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 32 p.
1987 Estimating density of dolphin schools in the eastern tropical Pacific ocean by line transect methods. Fish. Bull., U.S. 85:419–434.

Holt, R.S., and J.B. Cologne
1987 Factors affecting line transect estimates of dolphin school density. J. Wildl. Manage. 51(4):836–873.

Holt, R.S., and A. Jackson
1987 Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *McArthur* July 29–December 6, 1986. NOAA-TM-NMFS-SWFC-77, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 161 p.

Holt, R.S., and J.E. Powers
1982 Abundance estimation of dolphin stocks in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. NOAA-TM-NMFS-SWFC-23, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 95 p.

Holt, R.S., and S.N. Sexton
1987 Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *David Starr Jordan* July 29–December 5, 1986. NOAA-TM-NMFS-SWFC-76, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 171 p.

Holt, R.S., T. Gerrodette, and J.B. Cologne
1987 Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull., U.S. 85:435–446.

Perrin, W.F., M.D. Scott, G.J. Walker, and V.L. Cass
1984 Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Adm. Rep. LJ-87-02, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 68 p.

Richey, C.R.
1976 Memorandum of opinion. CA NO. 74-1465 and CA No. 75-0227 U.S. District Court, District of Columbia, May 11, 1976.

Smith, T.D.
1979 Report of the status of the porpoise stock workshop (August 27–31, 1979, La Jolla, CA). Adm. Rep. LJ-79-41, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 120 p.

SWFC
1976 Report of the workshop on stock assessment of porpoises involved in the eastern tropical Pacific yellowfin tuna fishery. Adm. Rep. LJ-76-29, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 60 p.

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Monitoring Trends in Dolphin Abundance in the Eastern Tropical Pacific using Research Vessels over a Long Sampling Period: Analyses of 1987 Data

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ABSTRACT

During 1987, the National Marine Fisheries Service conducted the second in its series of long-term research ship surveys to determine status of dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific. Line transect methodology was used by observers aboard two vessels for 120 days each. Relative abundance estimates of northern offshore spotted dolphins are approximately 1,300,000 animals with a coefficient of variation of 0.262. This estimate was larger than the 1986 estimate of 929,000 northern offshore spotted dolphins. Relative sizes of other stocks also varied. We examine reasons for these differences and discuss alternative methods of stratifying the data.

INTRODUCTION

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of those dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) (Richey, 1976). The status of the spotted dolphin, *Stenella attenuata*, is of special concern because it is the major species taken by the fishery (Smith, 1979). Of the spotted dolphins, the northern offshore stock is considered to be the most affected by the fishery because it has been fished more frequently than any other stock. The spinner dolphin, *S. longirostris*, and the common dolphin, *Delphinus delphis*, are also taken. The striped dolphin, *S. coeruleoalba*, and Fraser's dolphin, *Lagenodelphis hosei*, are occasionally caught but are difficult to distinguish from the other three species at a distance (Holt and Powers, 1982). These five species are herein grouped and termed target species.

In 1986, the NMFS initiated a research program to monitor relative abundance of dolphin populations in the ETP using two research vessels for at least five years during which six surveys will be conducted. The research design for the surveys, presented by Holt, Gerrodette and Cologne (1987), indicated that a 10% annual rate of decrease in northern offshore spotted dolphins could be detected (a total 41% decrease over six surveys) with alpha and beta error levels of 10%. Analyses of the 1986 data are presented by Holt and Sexton (1988a). In 1987, the NMFS conducted a second survey using the same vessels at the same time of the year. Herein, we present relative abundance estimates for the 1987 data and compare these to the 1986 estimates. We also discuss effects of several alternate stratification methods and data treatment factors on these estimates. Because we desire to determine change in population size over several years and not estimate absolute abundance, data from several years will eventually be used to select the most consistent relative indicator of population change.

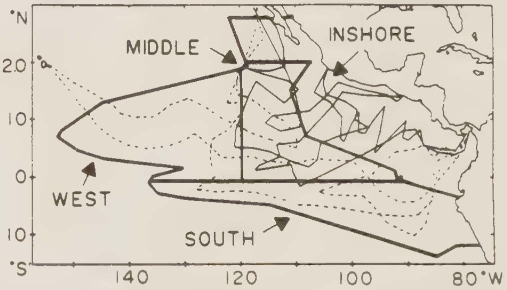

Fig. 1. Tracklines traversed by the NOAA R/V *David Starr Jordan* (solid) and *McArthur* (dash) during the 1987 survey. Tracklines generated using noontime positions.

MATERIALS AND METHODS

Study area and survey coverage

The study area and area strata were those used during the 1986 survey (Holt and Sexton, 1988a). The research vessels *McArthur* and *David Starr Jordan* traversed predetermined tracklines in the ETP from 30 July and 8 August, respectively, through 10 December (Fig. 1). Each ship was scheduled to spend approximately 120 days at sea but the *Jordan* departed 10 days late. Ship itineries, list of scientific personnel, survey equipment, data collection procedures and preliminary data summaries for each ship are presented by Holt and Sexton (1988b) and Holt and Jackson (1988). Only those factors important to this paper are presented here.

On each ship, two observers used 25X binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. A third observer served as data recorder and searched directly ahead of the ship when not recording data. Two teams of three observers each alternatively occupied the three duty stations. Each team was on duty for 2-hour shifts. During each shift, members spent approximately equal time occupying each duty station. Two of the six observers had completed several marine mammal cruises in the ETP and were experts in identifying marine mammals. These two identification specialists were assigned to separate teams such that one would always be on duty. Teams members did not change during the cruises. Observers switched ships at the mid-point of the cruises.

When possible, schools were approached and observers recorded independent 'best' estimates of school size. In some cases, an observer obtained a 'minimum' estimate but could not provide a best estimate. Independent estimates were averaged to obtain mean minimum and best estimates. When weather conditions were suitable, a *Hughes* 500D helicopter, based aboard the *Jordan* was used to photograph schools whose sizes were estimated by the observers. The photographs will be used to calibrate observer estimates of school sizes.

Abundance estimation

Relative estimates of population abundance of the target species (N_{ij}) were computed as (Holt and Sexton, 1988a):

$$N_{ij} = \sum_{k=1}^{4} (D_k S_{tk} P_{tk} P_{ik} A_k / A_{ik})(A_{ijk} + P'_{ij} A'_{ijk}), \quad (1)$$

where

D_k = estimate of density of schools of all dolphin species in area k,

S_{tk} = estimate of mean size of schools of all target species in area k,

P_{tk} = estimate of proportion of all dolphin schools which are target schools in area k,

P_{ik} = estimate of proportion of individuals of species i in target schools in area k,

P'_{ij} = estimate of proportion of individuals of stock j of species i in target schools in overlap region containing two stocks of species i (overlap region discussed in text),

A_k = total area inhabited by all target species in area k,

A_{ik} = area inhabited by species i in area k,

A_{ijk} = area inhabited by species i, stock j, in area k, and

A'_{ijk} = area inhabited by species i, stock j, in overlap region of area k.

The variance of N_{ij} was calculated using bootstrap methods. For each stratum, the number of legs of searching effort was tabulated and then effort legs equal to that number were randomly selected with replacement. This effort and the associated sightings were used to calculate school density, school size, species proportions and finally estimates of N_{ij}s. This was repeated 100 times. The variance of N_{ij} for each stock was calculated using these 100 estimates.

Formulae used to estimate school density are from Burnham, Anderson and Laake (1980), Holt (1985, 1987), and Hayes and Buckland (1983). The Fourier series (Cain *et al.*, 1979) and hazard rate (Hayes and Buckland, 1983; Buckland, 1985) models both provided adequate fits (similar point estimates and chi-square values) to the data but the hazard rate model was used because, unlike the Fourier series model, its use does not require subjective selection of the number of terms in the model and, therefore, could be used in the bootstrap procedures. Of schools containing both target and non-target species, only the proportion of individuals of the target species was used in the school size estimate. Estimates of the proportion of all dolphin schools that were target schools (P_{tk}) were calculated using formulae presented by Holt and Powers (1982). Formulae to estimate the proportions (P_{ik}) of the number of individuals for each species of all target individuals are given by Barlow and Holt (1986).

All species of dolphins encountered in the study area were included in the density analyses. Estimates were calculated using only schools containing 15 or more animals. Smaller schools were not used because we believe small schools both on and off the ships' tracklines may be difficult to detect especially during rough weather and may have been missed at a variable rate depending upon prevailing weather conditions (Holt, 1987).

Only schools detected within 3.7km (2.0 n.miles) perpendicular distance of the trackline were used to estimate school density because a 3.7-km truncation point provided the best fit of the model to this data. It was chosen because the perpendicular distance distributions of schools detected at greater distances were 'spiked' and because schools detected at greater than 3.7km have little effect on the density estimates. Schools detected at increasing distances from the trackline tend to include disproportionately more large schools because there is a direct correlation between the size of a school and the probability of it being detected (Drummer, 1985). This biases school size estimates upwards and species proportions toward species which occur in large schools. We attempted to adjust for this bias by weighting school size and species proportion estimates by the inverse of logarithm of school size (Holt and Powers, 1982). Finally, schools for which there were no 'best' estimates were not used in the school size or species proportion calculations.

Some stocks of the same species overlap geographic areas (A'_{ijk}). These overlapping stocks include (1) coastal and northern spotted, (2) eastern and whitebelly spinner and (3) Baja Neritic and northern common dolphins (Perrin *et al.*, 1984). The relative number of dolphins of each overlapping stock (P'_{ij}) was calculated for data pooled over strata. Because of small sample sizes, the pooled estimate of P'_{ij} was used in each of the bootstrapped iterations. For overlapping stocks of spotted dolphins and for spinner dolphins, the relative proportions of coastal and northern spotted and of eastern and whitebelly spinner stocks within their area of overlap were calculated as the averages of their relative abundances (percent occurrence). Few data were available to determine relative proportions of the overlapping Baja Neritic and northern common dolphins. Therefore, population estimates for Baja Neritic were combined with northern common dolphins.

The area inhabited by each target species (A_k) used to calculate the population abundance estimates were those defined by Au *et al.* (1979) and Perrin *et al.* (1984). The study area was partitioned into four strata (Holt and Sexton, 1988a). All four strata comprise the total area. The size of each stratum and the area occupied by each stock in each stratum was calculated by Holt and Sexton (1988a).

RESULTS

During the entire survey, observers aboard both vessels searched 28,611km and detected 1,249 marine mammal schools. Dolphins were present in 891 of these schools. While searching in the study area (Fig. 1), within 3.7km perpendicular distance of the trackline, and during Beaufort Sea states of 5 or less, observers on both vessels searched 26,519km and detected 352 dolphin schools (Table 1). The amount of effort and schools detected varied among strata; 42% of the total trackline searched and 53% of all schools detected were in the inshore area.

Table 1

1987 cruise data and results (see text). Data were truncated at 3.7km perpendicular distance. Schools with less than 15 animals were omitted from analyses. School sizes and species proportions were weighted by inverse of school size. Effort collecting during sea states 0 – 5 included in analyses. Data summed for both vessels. Total is for data summed over all four strata.

	Inshore	Middle	West	South	Total
Area (1,000km^2)	5,693	3,798	5,298	4,359	19,148
% Total area	30	20	28	22	100
Trackline searched (km)	11,145	7,974	3,529	3,871	26,519
% searching effort	42	30	13	15	100
Density ($\hat{D}_k$)[1]	4.74	3.15	2.16	3.58	3.75
No. schools detected[a]	187	89	27	49	352
Mean target species school size (S_{tk})	81.57	84.56	94.12	121.64	88.39
No. target schools[b]	151	77	23	38	289
Proportions:					
Target schools (P_{tk})	0.826	0.858	0.802	0.865	0.837
Spotted dolphins	0.284	0.524	0.367	0.319	0.360
Spinner dolphins	0.201	0.258	0.315	0.167	0.219
Common dolphins	0.272	0.009	0.056	0.080	0.152
Striped dolphins	0.242	0.159	0.046	0.295	0.214
Fraser's dolphins	0.000	0.050	0.217	0.139	0.055
Overlap area:					
Prop. Coastal Spotted					0.182
Prop. Offshore Spotted					0.818
No. Spotted schools					18
Prop. Eastern Spinner					0.677
Prop. Whitebelly Spinner					0.323
No. Spinner schools					83

[1] schools/1.000 km^2

[a] including unidentified dolphin schools.

[b] including schools identified as target species but for which a best estimate of school size was not made.

Table 2

Estimates of population sizes (N_{ij}) (in thousands of animals) by stock for target species in total area. Values given are weighted by stratum.

Species/stock	N_{ij}	SE(N_{ij})	CV(N_{ij})
Spotted			
Coastal	32.4	6.8	0.210
Northern Offshore	1,275.4	334.3	0.262
Southern Offshore	501.8	199.8	0.398
Total	1,809.6	540.9	0.299
Spinner			
Costa Rican	17.9	4.6	0.257
Eastern	533.2	149.8	0.281
Northern Whitebelly	334.2	96.9	0.290
Southern Whitebelly	252.2	105.1	0.417
Total	1,137.5	356.4	0.313
Common			
Northern Tropical	130.3	47.7	0.366
West Central Tropical	53.0	44.8	0.845
East Central Tropical	307.0	112.0	0.365
Southern Tropical	201.0	110.7	0.551
Total	691.3	315.2	0.456
Striped			
Northern Tropical	124.4	23.0	0.185
West Central Tropical	33.7	23.8	0.706
East Central Tropical	353.9	63.1	0.178
Southern Tropical	584.2	147.8	0.253
Total	1,096.2	257.7	0.235
Fraser's	451.0	282.5	0.626
Total	5,185.6	1,752.7	0.338

The estimate of f(0) for data in the total area was 0.577. Density estimates (D_k) in the four strata, calculated using the pooled f(0), ranged from 2.21 to 4.84 schools/1000km^2 (Table 1). Estimates of mean school size (S_{tk}) of target species ranged from 81.57 to 121.64 animals (Table 1). The proportion of identified dolphin schools that included target species (P_{tk}) ranged from 0.826 to 0.900 among strata (Table 1).

The proportions of individuals of target species that were spotted dolphins (P_{ik}) ranged from 0.284 to 0.524 among the strata (Table 1). The proportions of the other target species among strata also varied greatly. For example, the proportion of common dolphins ranged from 0.009 to 0.272 (Table 1). Only 18 spotted dolphin schools were detected in the overlap region of the coastal and offshore spotted stocks. The proportion (P'_{ij}) of these that were offshore spotted dolphins was 0.818 (Table 1). Of 83 spinner dolphin schools detected in the area of overlap of eastern and whitebelly spinner stocks, 0.677 were eastern spinner dolphin schools

The estimate of relative abundance for each stock of the target species is presented in Table 2. Spotted dolphins were the most abundant target species. The estimate of 1,275,400 northern offshore spotted dolphins represented 70% of the estimate of all stocks of spotted dolphins. The coefficient of variation of the abundance of the northern offshore spotted stock, CV(N_{ij}), was 0.262. The abundance estimate for eastern spinner dolphins was 533,100 animals with a CV of 0.281.

DISCUSSION

Abundance estimates may be calculated using equation (1) by pooling variables across geographical strata and/or species categories. In general, the greater the degree of pooling across variables, the more precise (lower CVs) but also the more biased are estimates of abundance. For example, we calculated the density estimate (D_k) by pooling perpendicular distance distributions across strata such that

$$D_k = \sum_{k=1}^{4} n_k f(0)/2l_k.$$

where n_k is the number of dolphin schools detected in stratum k and l_k is the line length searched in stratum k.

An alternate method was examined which calculated f(0) for data in each stratum. This yielded an abundance estimate for northern offshore spotted dolphins of 1,576,600 animals compared to our estimate of 1,275,400 animals (Table 2) but the estimate of CV was 0.363 compared to 0.262 for our pooled f(0) method. The larger CV resulted because the hazard rate model was applied to small data sets in the south (27 schools) and west (49 schools) strata (Table 1).

We also investigated another alternate method by calculating abundance estimates for all variables in equation (1) pooled across all geographic strata. For the northern offshore spotted dolphins, this yielded an abundance estimate of 1,497,200 animals with a CV of 0.158. Although the estimate is very precise, it may be biased upwards because encounter rates were highest in the inshore stratum (Table 1) which received 42% of the total survey coverage but only represented 30% of the total geographic area.

We calculated school density using schools of all dolphin species; then calculated the proportion of those schools which were target species; and finally calculated the proportions of individuals of each species in the target species [equation (1)]. However, two alternate methods were investigated. They were to (1) calculate school density using only schools of target species and prorating to each species and (2) calculate abundance estimates using only data for each individual species. Method 1 does not require calculation of the proportion of all schools that are target schools, however, it utilises smaller samples than our method and a proportion of the unidentified schools must be allocated to the perpendicular distance distribution to calculate school density. We calculated the proportion of identified target schools in each perpendicular distance interval and then assigned that proportion of the unidentified schools detected in the interval to that interval.

Method 2 does not require calculation of species proportions but it utilises very small data sets. Sufficient data only exists to calculate estimates for spotted and spinner dolphins. In this method, we assumed no unidentified dolphin schools contained spotted dolphins.

Estimates of northern offshore spotted dolphins using methods 1 and 2 were 1,235,300 (CV 0.265) and 1,119,600 (CV 0.320) animals, respectively. The estimate for method 2 may have been smaller than both the method 1 estimate and our estimate of 1,275,400 animals using all dolphin schools (Table 2) because it did not include any unidentified schools. However, based on field experience the senior author believes that spotted dolphin schools rarely are not identified. CV estimates were similar for method 1 and our method (0.265 and 0.262, respectively) but both were smaller than the method 2 CV (0.320) which was based on small samples.

Abundance estimates calculated using all dolphin species and data pooled over all strata (total area in Table 1) may provide the most consistent *relative* abundance estimates during the six surveys. The method provides very precise estimates (CV for northern offshore spotted dolphins was 0.158 compared to our estimate of 0.262) because it avoids calculating estimates using small sample sizes. However, the abundance estimates may be biased upwards because proportionally more effort is expended in the high density inshore area (42%) compared to its relative size (30% of total survey area). This bias is acceptable if survey coverage among strata is relatively constant during all surveys as it was during the first two surveys. During 1986, the percents of the survey effort in the inshore, middle, west and south strata were 43, 28, 14 and 15%, respectively (Holt and Sexton, 1988a) and in 1987 they were 42, 30, 13 and 15%, respectively (Table 1).

The estimate of abundance for northern offshore spotted dolphins during 1987 was larger than the 1986 estimate. The 1986 and 1987 estimates were 929,000 (Holt and Sexton, 1988a) and 1,275,400 (Table 2) animals, respectively. These estimates were not statistically different ($p>0.01$). The larger 1987 estimate occurred because school density increased in 1987 in all strata. In addition, the proportion of spotted dolphins in the target species increased in the middle stratum. The 1986 estimates for density in the inshore, middle and west strata were 3.62, 2.56, and 1.89 schools/1000km^2, respectively (Holt and Sexton, 1988a); the corresponding 1987 estimates were 4.74, 3.15 and 2.16 schools/1000km^2, respectively (Table 1). The proportion of spotted dolphins of the target species in the middle stratum increased from 0.378 in 1986 to 0.524 in 1987. However, the proportion of all dolphins that were target species in the middle stratum slightly decreased from 0.906 in 1986 to 0.858 in 1987. In addition, school size estimates decreased slightly in the inshore and west strata and remained constant in the middle stratum. Estimates during 1986 in the inshore middle, and west strata were 89.41, 83.97 and 104.55 animals, respectively (Holt and Sexton, 1988a); in 1987 they were 81.57, 84.56 and 94.12 animals, respectively (Table 1).

The reason for the larger 1987 abundance estimate for northern offshore spotted dolphins may be attributed to sampling variability among surveys. Another factor is that dolphins in the south stratum during 1986 may have migrated into the northern strata during 1987. However, although the mean school size in the south stratum decreased from 179.04 animals (Holt and Sexton, 1988a) during the 1986 survey to 121.64 animals for 1987 survey (Table 1), the density estimate in the south stratum increased from 2.32 schools/1000km^2 in 1986 to 3.58 schools/1000km^2 in 1987. In addition, the proportion of target individuals that were spotted dolphins increased from 0.170 to 0.319. In fact, the abundance estimate for southern offshore spotted dolphins also increased (from 218,500 animals in 1986 to 501,800 animals in 1987).

Abundance estimates for the southern stocks varied greatly between 1986 and 1987. For example, the estimate for southern common dolphins was 943,200 animals during 1986 (Holt and Sexton, 1988a) but was 201,000 animals (Table 1) during 1987. This was because the proportion of common dolphins in the south stratum decreased from 0.661 during 1986 (Holt and Sexton, 1988a) to 0.080 during 1987 (Table 1). Estimates for the other species exhibited corresponding changes. This variability was because estimates in the south stratum were based upon few sightings. During 1986 and 1987, only 27 and 38 target schools, respectively, were detected in the south stratum. Species proportions in the west stratum were also based on few schools (Table 1) which may have yielded variable estimates for the western stocks.

Although estimates for some stocks varied greatly between years, the abundance estimates for all target species summed were similar. The 1986 and 1987 estimates for all target species were 4,471,200 (Holt and Sexton, 1988a) and 5,185,600 (Table 2) animals, respectively. The 1987 estimate is 16% larger than the 1986 estimate.

Selection of the best option to determine population changes will be investigated with additional years' data. We will also investigate several factors which may have contributed to differences observed between surveys. These include ship effects, observer variability, sea state effects and survey coverage variability (Holt and Cologne, 1987).

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REFERENCES

Au, D., Perryman, W.L. and Perrin, W. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-79-43. 59pp

Barlow, J. and Holt, R.S. 1986. Proportions of species of dolphins in the eastern tropical Pacific. US Dep. Commer., NOAA-TM-NMFS-SWFC-56. 44pp.

Buckland, S.T. 1985. Perpendicular distance models for line transect sampling. *Biometrics* 41: 177–95.

Burnham, K., Anderson, D. and Laake, J. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* No. 72: 202pp.

Crain, B., Burnham, K., Anderson, D. and Laake, J. 1979. *A Fourier Series Estimator of Population Density for Line Transect Sampling*. Utah State Univ. Press, Logan. 25pp.

Drummer, T.D. 1985. Size-bias in line transect sampling. PhD Dissertation, Univ. Wyoming, Laramie, WY.

Hayes, R.J. and Buckland, S.T. 1983. Radial distance models for the line transect method. *Biometrics* 39: 29–42.

Holt, R.S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20. 32p.

Holt, R.S. 1987. Estimating density of dolphin schools in the eastern tropical Pacific ocean by line transect methods. *Fish. Bull., US* 85(3):419–34.

Holt, R.S. and Cologne, J.B. 1987. Factors affecting line transect estimates of dolphin school density. *J. Wildl. Manage.* 51(4):836–73.

Holt, R.S., Gerrodette, T. and Cologne, J.B. 1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. *Fish. Bull., US* 85(3): 435–46.

Holt, R.S. and Jackson, A. 1988. Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *McArthur* July 30 – December 10, 1986. US Dep. Commer., NOAA-TM-NMFS-SWFC-116. 143pp.

Holt, R.S. and Powers, J.E. 1982. Abundance estimation of dolphin stocks in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. US Dep. Commer., NOAA-TM-NMFS-SWFC-23, 95pp.

Holt, R.S. and Sexton, S.N. 1988a. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: Analyses of 1986 data. In Review. (submitted to Fish. Bull.).

Holt, R.S. and Sexton, S.N. 1988b. Report of a marine mammal survey of the eastern tropical Pacific aboard the Research Vessel *David Starr Jordan* August 8 – 10 December, 1987. US Dep. Commer., NOAA-TM-NMFS-SWFC-117. 137pp.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1984. Review of geographical stocks of tropical dolphins (*Stenella spp.* and *Delphinus delphis*) in the eastern Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-87-02, 68pp.

Richey, C.R. 1976. Memorandum of opinion. CA NO. 74–1465 and CA NO. 75–0227 US District Court, District of Columbia, May 11, 1976.

Smith, T.D. 1979. Report of the status of the porpoise stock workshop (August 27–31, 1979, La Jolla, CA). Southwest Fish. Cent. Adm. Rep. No. LJ-79-41, 120pp.

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Activity Patterns of Striped Marlin in the Southern California Bight

David Holts and Dennis Bedford

The billfish resource along the west coast of Mexico and California is important to both commercial and recreational fisheries. In Mexico, the striped marlin *(Tetrapturus audax)*,is taken in large quantities by commercial longline vessels and by recreational fishermen (Squire and Au 1989). In California, the striped marlin is considered to be among the most desirable of big-game fishes. Although not taken off California in numbers comparable to landings from Mexican waters, it nevertheless supports a very valuable recreational industry (Squire 1987a). In recognition of its value to California's sport fishing public, the striped marlin has been legally designated as a game fish for "sport only" utilization and cannot be taken or possessed by commercial fishermen, or imported into California fish markets. The California Department of Fish and Game (CDFG) has documented increased fishery interactions and conflicts in recent years between recreational and commercial fishermen. Tensions between recreational groups and the commercial fishing industry have increased with the expansion of the drift gill-net fisheries for thresher shark *(Alopias vulpinus)* and swordfish *(Xiphias gladius)* in the late 1970s and early 1980s (Beford and Hagerman 1983, Beford 1987).

Knowledge of striped marlin activity patterns, such as vertical and horizontal swimming patterns, variability of swimming speeds, and temperature-depth preferences, can provide fisheries managers with essential information needed for resolving user conflicts. Acoustic telemetry has been used to monitor the behavior patterns and physiological characteristics that influence habitat preference of large free-swimming pelagic fish (Holland et al 1986, Yuen 1970, Yuen et al 1974, Carey and Robison 1981, Carey and Olson 1981, Yonemori 1982). The current studies with striped marlin are, in part, designed to determine their behavior and vulnerability to various types of commercial and recreational fishing gears and to gain information on the availability of striped marlin off southern California. The correlation of behavioral patterns with various environmental parameters can also be valuable in stock assessment and distribution studies.

During September, 1982, biologists with the National Marine Fisheries Service (NMFS) succeeded in tagging with a sonic tag and tracking a striped marlin (SM82-1) for a period of 24 hours off the coast of southern California. Four years passed before another attempt was made. In 1986, the CDFG recognized the need for information on the behavior of striped marlin as part of studies concerned with incidental catches by the drift gill-net fishery for swordfish. A cooperative research project between the CDFG's Marine Resources Division and the NMFS' Southwest Fisheries Center's Pelagic Fisheries Resources Division was established in 1986 to track striped marlin off southern California. During the summers of 1986 and 1987, ten striped marlin were tagged with sonic transmitting tags and their movements tracked. Results of this project to date are reported herein.

Methods

The tracking vessel was the 59-foot sport fishing boat, *"Pacific Clipper,"* under contract to the CDFG. It accommodated a scientific crew of up to six, with ample space for fishing, tagging, and tracking equipment. Our tagging and tracking equipment consisted of Vemco* V4P sonic transmitter tags, CS-40 directional hydrophone and a VR-60 receiver-decoder, all similar to that described by Holland et al (1986).

The depth transmitters came in two full-scale pressure ranges of 0 to 100 psi and 0 to 1,000 psi. Depth sensitivity was subject to 2 percent error at full scale. The 1,000 psi tags were used initially, until we established that striped marlin tended to stay in the upper portion of the water column. Output frequencies were set at 29.00 and 34.00 kHz; anticipated battery life was 7 to 14 days, depending on the depth of the fish. The transmitted signal was received through a directional hydrophone, bolted to a rotatable shaft, and was attached to a control motor which turned the hydrophone up to 180 degrees in either direction. This assembly was mounted amidships on the starboard side of the vessel's hull. The rotational control unit for the hydrophone was operated from inside the cabin. A plastic PVC faring was mounted over the hydrophone to reduce external noise while underway at speeds of up to 6 knots.

The receiver digitized the telemetered pulses and stored both time and depth data for later transfer to a computer. The receiver's audible signal was recorded on cassette data tapes as a back up in case any problems ocurred with the internal data storage memory. The strength of the signal received was used to estimate the distance to the target, thus allowing the tracking team to maintain a desired distance from the tagged fish. We estimate our normal operating distance from the fish was approximately 200 to 400 m (650 to 1,300 ft) and our maximum range from which we could receive the signal was about 800 m (2,600 ft).

During tracking, the vessel's location was recorded at 15 minute intervals through the use of Loran-C. Since the distance from the vessel to the fish was routinely kept under 400 m (1,300 ft), the location of the vessel was assumed to be the same as the fish.

During tracking, XBT (expendable bathythermograph) casts were taken to obtain water temperature profiles at intervals of approximately 6 hours.

Fishing and tracking operations were conducted in the most promising areas as determined by daily angler success rates. Cruise dates were scheduled to coincide with recreational marlin tournaments whenever possible. Sport fishing clubs and tournament organizers were asked for assistance in catching marlin for tagging. All but two of the fish were caught and donated by sport fishermen.

When an angler notified the *"Pacific Clipper"* that a fish was hooked-up, and would be donated, a course and distance to the donor vessel was plotted. If we could reach the donor vessel in the time it would take to bring the marlin alongside the catcher vessel we would proceed at top cruising speed to that location. Once alongside, a tagging team would be sent by rubber raft to board the donor vessel and tag and release the fish. The weight of each fish was estiamted at the time of release.

Results

In all, 11 striped marlin were tagged and tracked (including the fish tracked in 1982; SM82-1). Three of the marlin were tracked for less than 5 hours and eight were tracked from 20 to 48 hours (Table 1). Only those tracks with durations of 20 hours and longer are included in the analysis. Marlin tracks lasting 20 hours

Table 1. Tagging and tracking statistics for 11 striped marlin.

Fish	Date	Weight (estimated) kg	Location	Time tracked hrs	Distance traveled		Donated by skipper
					nm	dir	
SM82-1	9/22/82	55	425 spot	24	24	WSW	NMFS
SM86-1	9/27/86	50	Avalon	24	37	S	H. Sutton
SM86-2	10/01/86	55	Mackerel Bank	3	5.5	S	—
SM87-1	9/13/87	50	East of Slide	3.5	4	E	G. Stotesbury
SM87-2	9/16/87	70	East of Slide	20	22	SE	NMFS/CDFG
SM87-3	9/17/87	70	East of Slide	48	57	SE	J. Belus
SM87-4	9/25/87	55	14-mile Bank	24.5	31	E	W. Woodard
SM87-5	10/02/87	80	267 spot	30.5	44	S	G. Jasper
SM87-6	10/04/87	—	267 spot	24	23	NW	G. Jasper
SM87-7	10/17/87	—	267 spot	4.5	6	SW	D. Denholm
SM87-8	10/19/87	65	Dana Point	24.5	16	S	R. Rafkin

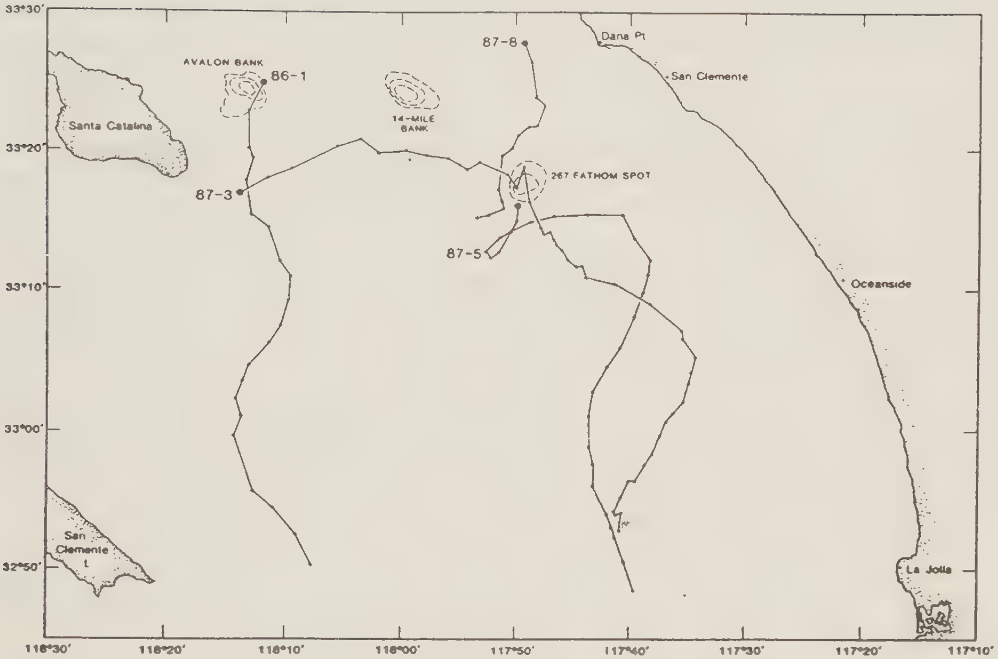

Figure 1. Horizontal movement of four striped marlin generally showing a predominant movement away from the tagging area and in a southward direction. Dots along the track lines indicate intervals of approximately one hour.

or more totaled 219.5 hours and covered 258 nautical miles within the southern California Bight (Figs. 1 and 2). Individual activity and depth profiles for seven of the striped marlin tracked are shown in Figure 3.

Summary of Striped Marlin Tracks

SM82-1. This 55-kg (120 lb) fish was caught on an artificial lure trolled from the tracking vessel 28 miles southwest of Point Loma, San Diego, on September 22, 1982. This marlin was brought to the vessel in 23 minutes, tagged just below the dorsal fin, and released at 1130 hrs in excellent condition. It immediately descended to 25 m (80 ft) and moved north 1.5 nm in the next hour. The fish continued traveling north at a depth of 8 to 10 m (26 to 32 ft) for three more hours. It became relatively inactive at sunset, until shortly after 2100 hrs when it made a short dive to 30 m (100 ft) and began moving west to southwest at about 1.0 knot (kt). The fish stayed at 5 to 10 m (16 to 32 ft) and continued in the same westward direction for the next 17 hours. It made four dives to at least 35 m (104 ft) between midnight and sunrise. The fish traveled an average of 1.0 kts while moving 24 nm in the 24-hour track. Its maximum speed was recorded at 2.0 kts during the midmorning hours. The fish remained in 21°C (70°F) water throughout most of the track. Nearly 86% of the tracking time was spent in the well-mixed surface water above 10 m (32 ft). Its deepest dive to 75 m (244 ft) occurred just after 0200 hrs. The temperature was 12.5°C (54.5°F). Only 3% of the tracking time was spent below 40 m (130 ft).

SM86-1. This 50-kg (110 lb) marlin was caught September 27, 1986, on an artificial lure and donated to our research by a tournament participant. It was tagged and released in good condition at 1230 hrs on the Avalon Bank, located six miles east of Avalon, Santa Catalina Island. This fish remained within 5 m (16 ft) of the surface as it began moving south. The fish continued south for 37 nm at an average speed of 1.5 kts, varying between 0.5 and 3.5 kts. Just after sunset, this marlin descended to 20 m (65 ft) and maintained that depth for 6 hours. Between 0100 and 0400 hrs it made a series of dives between 5 and 30 m (16 and 98 ft). It spent 63% of the tracking period at or above 12 m (39 ft). During the daylight hours, only 10% of its time was below 12 m (39 ft). During nighttime hours, it spent nearly 80% of the time

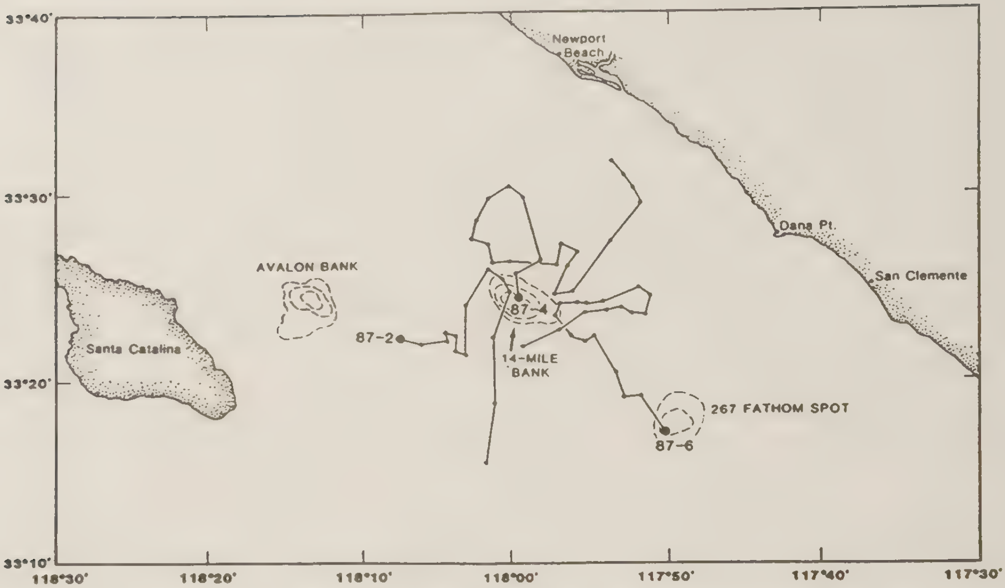

Figure 2. Horizontal movement of three striped marlin showing considerable movement but without leaving the tagging area. Dots along the track line indicate intervals of approximately one hour.

below 12 m (39 ft), with four short descents below 40 m (130 ft). The period of least movement occurred between the hours of 0400 and 0700, although it made two short dives to 40 m (130 ft). The fastest sustained speed was 2.0 and 3.5 kts during the last 6 hours of the track.

SM86-2. This 55-kg (121-lb) fish was tagged and released near the west end of San Clemente Island at 1100 hrs on August 1, 1986. It was tracked for only 13 hours, when the signal was lost due to a damaged hydrophone wire. Replacement of the defective hydrophone took approximately 30 minutes, but efforts to relocate the fish were unsuccessful. This striped marlin traveled 5.5 nm in a southward direction and stayed very near the surface during the tracking period.

SM87-1. This 50-kg (110-lb) fish was donated by a tournament participant and tagged and released off the east end of Catalina Island at 1143 hrs, September 13, 1987. This fish was exhausted when released but otherwise in good condition. It was tracked for just over 3 hours in an eastern direction before it was lost due to a malfunctioning hydrophone. The average speed was 1.2 kts over the period.

SM87-2. This 70-kg (155-lb) marlin was caught on a jig trolled behind the tracking vessel, and was tagged and released in good condition at 1530 hrs near the east end of Catalina Island on September 16, 1987. It was tracked for 22 nm over the next 20 hours. For the first 2 hours of the track it remained within 1 mile from the point of release at a depth of 10 m (33 ft). It then began moving east by northeast at about 1 kt, at a depth varying between 20 and 33 m (65 and 107 ft). Between midnight and sunrise, it passed slowly (0.6 kts) over the top of the "14-Mile Bank," also known as Lasuen Knoll, at a depth of 10 m (33 ft). It turned south in the early morning and maintained 2.3 kts for over 2 hours. Its deepest dive was to 55 m (180 ft) just after sunset. It spent 100% of its daytime hours in the mixed layer, but only 61% of its nighttime hours were in the mixed layer.

This marlin was observed twice during the track. It was seen jumping or "greyhounding" just 4 hours after release, presumably in an attempt to shake the tag off its back. At 1100 hrs the following morning, we observed the fish actively feeding on surface schools of anchovies for over 20 minutes. The fish began swimming south after feeding. The track had to be terminated when the fish entered a military restricted zone.

SM87-3. This 70-kg (154 lb) marlin was donated by a tournament participant 3 miles off the east end of Catalina Island. It was released

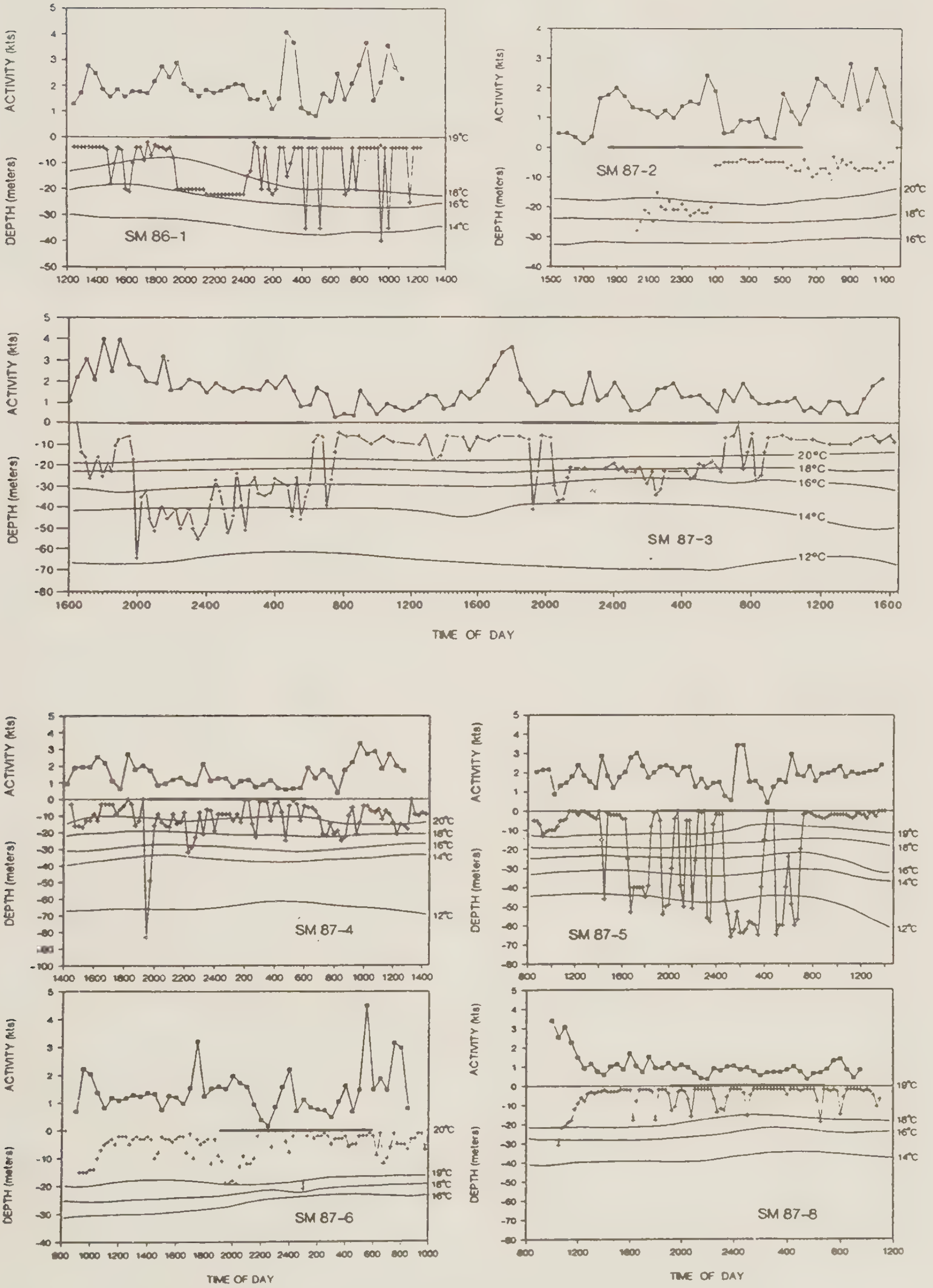

Figure 3. Activity and depth profiles for seven striped marlin tracked at least 20 hours. Activity data (knots) were taken from position data every 15 minutes and smoothed with a running average over 45-minute periods. Depth data were likewise smoothed over 15-minute periods to accommodate computer graphics and may not indicate precise depths attained by individual fish.

at 1615 hrs on September 17, 1987, and tracked for 48 hours and 57 nm. It began moving northeast at 1.8 kts and then altered course to east at 2100 hrs and remained on this heading until 0400 hrs. It made its deepest dive shortly after sunset (2038 hrs) to a depth of 93 m (305 ft). It returned to a depth of about 40 m (131 ft) within 4 minutes and began making numerous vertical excursions between 25 and 65 m (80 and 210 ft) during the nighttime hours. At sunrise it assumed a depth of 6 to 7 m (21 ft) for the remainder of the day. Horizontal movement decreased to between 0.5 and 1.0 kts during the first 10 hours of daylight and then increased to 3.0 kts in the late afternoon, when the fish began "tailing" (tail seen breaking surface while swimming) down-swell. The fish made two dives to nearly 40 m (131 ft) just after sunset and continued southeast and east at a depth of 20 to 30 m (66 to 98 ft) and speed of 1.0 kt during the rest of that evening. The following morning, it again ascended to a depth of 6 to 7 m (20 to 23 ft). The marlin increased its speed to over 2 kts in the second afternoon and was lost when it began tailing down-swell.

This fish was seen several times during the tracking period. It jumped twice three hours after we began tracking, and jumped again several times the following afternoon. Following this jumping display it was observed "tailing" down-swell. The next morning it jumped several more times and "finned" at the surface for about 20 minutes. That afternoon it was again seen "tailing" down wind. This marlin was most active in the afternoons and appeared least active in early mornings.

SM87-4. This 55-kg (121 lb) marlin was tagged at the "14-Mile Bank" at 1358 hrs, September 15, 1987, and tracked for over 24 hours and 31 nm. After release it descended to 24 m (79 ft) for almost two hours, then ascended to 10 m to 15 m (33 to 49 ft) and began moving to the north at about 1.0 kt. It made a short dive to 90 m (295 ft) just after sunset and then returned to between 20 and 30 m (66 and 98 ft). During the evening it moved west, along a warm temperature front and then southwest and finally south into cooler, 18°C (65°F) surface water. At 2300 hrs, it began moving east at 1.0 kt and continued with several short dives until sunrise. Here it remained inactive for an hour and then proceeded north in the warmer surface waters and within 3 nm of the beach. The time spent between 20 to 30 m (66 to 98 ft) increased during the first hours of daylight. This marlin spent 76.7% of its time below the warm mixed surface layer. It did not appear to spend any more time at depth during the night than it did during the day. At 0700 hrs the fish was observed swimming and feeding with four other marlins. It appeared most active in the early mornings and late afternoons. This fish was lost in the afternoon when it turned down-swell and increased speed.

SM87-5. This 80-kg (176-lb) marlin was donated by a sport fishermen on October 2, 1987, approximately 20 nm southwest of Newport Beach, near a high spot on the local charts called the "267 Spot" (267 fathoms). This was one of the largest marlin tracked and was bait-caught and "tail-wrapped" (the fishing line wrapped around its tail). Although landed tail first and exhausted, it was released at 0827 hrs and tracked for over 30 hours and 44 nm. When released, it descended to 10 m (33 ft) and began moving south at 1.5 kts). In the early afternoon, it reversed its direction and began moving northeast. This marlin made two dives to 55 m (180 ft) in the afternoon.

During the second of these two dives (at 1730 hrs), it approached a commercial drift gill net, of the type used to catch swordfish. The fish approached the net at a depth of 50 m (162 ft), a depth which could have resulted in entanglement. As the tracking vessel neared the buoy line of the net, it appeared that the fish had stopped moving forward. The tracking vessel passed over the top of the gill net, the cork line hanging 5.5 m (18 ft) below. After crossing, the directional hydrophone rotated 180 degrees back in the direction of the net. The marlin was still there. It became evident after a few minutes that the fish was slowly moving on a course parallel to the length of the gill net. The tracking vessel's electrical power failed at this juncture. The signal was lost for 8 minutes while the receiver was connected to an alternate power supply. Immediately after the power was returned, and the signal regained, we discovered the marlin passing the tracking vessel, on its previous heading but at a depth of only 10 m. Apparently, it had been able to detect the presence of the net and, eventually, after a fair amount of hesitation, swam over or under the net. We are unable to say for sure which happened, as the signal and fish were lost during this critical period.

The marlin turned east at sunset and maintained a speed of 2 kts until it encountered cooler surface water at 2400 hours. After an hour of inactivity, it resumed swimming to the southeast averaging 1.6 kts as it moved along a band of cooler water. In the 4 hours preceding sunrise, it turned south and traveled between 1 and 2 kts while making several dives to 50 and 60 m (163 and 195 ft). Three of these dives lasted from 30 to 100 minutes. Only one dive was made after sunrise and the fish remained near the surface for the remainder of the tracking period. It spent 79% of the daylight hours in the mixed layer above 20 m (65 ft) and 56% of the nighttime hours below 20 m (65 ft). It was observed at the surface the following morning, accompanied by one other marlin, with both their tails protruding above the water's surface.

SM87-6. This angler-donated fish was released in good condition at 0930 hrs on October 4, 1987. The fish remained at 13 m (42 ft) for the first hour as it began moving north. It remained at 3 to 5 m (10 to 16 ft) depth for the next 4 hours, maintaining a speed of about 1.0 kt. It made a 2-hr dive just after sunset that varied in depth between 15 and 24 m (49 and 78 ft). It then ascended to 5 to 8 m (16 to 26 ft), while continuing northeast and toward shore. The fish reversed its direction between midnight and sunrise and moved off shore, remaining very close to the surface. There were several short 1- to 2-minute dives to 14 to 18 m (45 to 58 ft) as it returned to the "14-Mile Bank." This marlin spent a total of 97% of its time in the mixed layer. The fish was seen "tailing" with one other marlin, just before we lost contact with it at midmorning. This marlin was most active in the afternoon and least active in the pre-dawn hours.

SM87-7. This fish was another angler-donated marlin tagged near the "14-Mile Bank" and released at 1030 hrs on October 17, 1987. This fish moved steadily south and southwest while staying in the upper 3 m (10 ft) of water. It jumped several times, at 1.5 hours after tagging. The fish was lost after moving 6 nm in 4.5 hours.

SM87-8. This 65-kg (143 lb) marlin was tagged and released at 1020 hrs just off Dana Point on October 19, 1987. It was judged to be in "fair" condition at tagging, as it had everted and reswallowed its stomach prior to being landed. It descended to 20 m (65 ft) for the first hour after release and then returned to 6 to 10 m (20 to 33 ft) for the following 2 hours, all the while moving at 1.4 kts to the south-southwest. Turning south at 1500 hrs, it continued at 1.0 kt and a depth of 2 to 4 m (6 to 10 ft) with occasional descents to 15 to 18 m (49 to 59 ft) for the rest of the track. The fish remained inactive from 2300 hrs until just after sunrise. This marlin spent 97% of the track in the mixed layer and 77% of the track was spent at less than 10 m (33 ft). It exhibited no depth difference between day and night.

General Behavior of Striped Marlin

No single repetitive behavior was found to be characteristic of all the marlin tracked during this study. It is possible, however, to make a few generalizations about striped marlin behavior in the waters off southern California. These may be classified into three broad categories for discussion: (1) occasional behaviors for which there may be only one or two observed occurrences, (2) periodic behaviors which seem to occur only during predictable times of the day or night and (3) behavioral responses to environmental parameters.

Occasional Behavior

Feeding. Striped marlin are efficient predators and feed on schools of northern anchovies *(Engraulis mordax)*, Pacific saurys *(Cololabis saira)*, and the jack mackerel *(Trachurus symmetricus)*, as well as smaller members of the mackerels and tunas from the family Scombridae (Eldridge and Wares 1974). Two marlin (SM87-2 and SM87-4) were observed feeding during mid- to late-morning hours following the first night of tracking. Each episode lasted for about 20 minutes. Both marlin were observed slicing through balls (surface schools) of anchovies, dorsal fins breaking the surface briefly as they flashed by. These fish appeared to be taking large mouthfuls of anchovies while charging through the bait schools. We did not observe any evidence of the bill being used as a weapon, although our vantage point limited these observations only to surface activity.

On several occasions, following late-night periods of inactivity, a fish would suddenly dive, from the surface to depths as great as 40 m (130 ft), and made rapid changes in direction. We can not be sure if such behavior resulted from the fish being startled by our presence or if this, too, could have been actual feeding. Since none of these fish were subsequently recovered for examination of stomach content, we are left to speculate as to the true nature of this behavior.

Periodic Behaviors

Breezing. On several occasions we observed a behavior from both tagged and non-tagged marlin which has been described by fishermen as "breezing" or "tailing." The first name is derived from the fact that this behavior seems to occur only when the wind is blowing, usually in the afternoon. In the Southern California Bight there usually is an onshore breeze in the afternoon during the summer. The second name describes what the observer actually sees as the fish swims by.

During the afternoon breeze, marlin can be seen swimming rapidly down-wind and down-swell. This is characterized by significantly increased speed and a change in direction to correspond roughly to the wind direction. The fish can be seen swimming down-swell at the leading edge of a wind wave, with the upper portions of their caudal fins protruding from the water. While they can only be seen gliding down-swell for up to a couple minutes at a time, this activity may continue for as long as 4 hours and include occasional dives to 20 m (SM86-1 and SM87-5). Swimming speeds as great as 5 or 6 kts may be sustained for short periods. Not coincidentally, most of the tagged fish which evaded our tracking efforts were lost during this activity. A miscalculation of distance from the fish, or a wrong turn, provided the crew with little time to recognize and correct the error before the fish was no longer within signal range.

Sleeping. During the late night and early morning hours, including the period just after sunrise, some fish went through periods of inactivity which we termed "sleeping" behavior. This is characterized by little or no horizontal movement or vertical excursions beyond 5 to 10 m. During these periods, lasting from one to several hours, the fish would remain motionless, just below the surface of the water. Occasionally at sunrise, the tail and dorsal fin could be seen on non-tagged marlin as well as the tagged fish. All fish displayed some slowing of activity during the night hours, although not all fish went through periods of complete inactivity. One fish (SM87-3) exhibited this behavior between 0800 and 1200 hrs, an exception to the time this behavior was generally observed. One other fish exhibited a marginal form of this behavior. Marlin SM87-4 reduced its activity for 4 hours but made three vertical dives to at least 30 m (98 ft) during the period.

Social behavior. Small aggregations of marlin were observed displaying the behavior we previously described as "sleeping." We noted such aggregations during fishing operations, and on two occasions the tagged marlin joined other non-tagged marlin, forming a small group. Once, while we were tracking it, SM87-4 was joined by three other marlin. Several groups of up to 10 marlin were observed with the tagged marlin. SM87-5 was also joined by one other marlin at 0800 hrs the morning after tagging. While such gatherings were observed only during these early morning "sleeping" episodes, or afternoon breezing activity, commercial swordfish spotter pilots have reported that large groups of striped marlin are often seen just below the surface during mid-day, as well.

Environmental Responses

Horizontal displacement. The horizontal movements of striped marlin in this study fall into two groups. There were those that left the area following tagging (Fig. 1), and others that remained in the same general locality where they were first captured (Fig. 2). Five of the eight fished tracked for 20 hours or longer left the area, swimming on a heading ranging from southeast to southwest. The other three marlin followed paths which reversed course or even crossed over a previous track. We did not find, within our study period, that season played any role in predicting whether a fish would leave the area, although the general movement of all fish in a southward direction suggests that migration may play a role.

Relatively large distances were covered, in all cases, considering the time intervals, ranging from 16 nm to 57 nm. The average speed for all tracked marlin was 1.24 kts and the individual average ranged between 0.75 and 1.54 kts. This compares favorably with the top speed, 1.07 kts, reported by Squire (1987b) for striped marlin tagged with conventional tags off southern California, and recovered between 0 and 60 days later. The eight marlin tracked over 20 hours spent an average of 28% of track time at a speed of less than 1 kt and 17% of their time over 2 kts. None was tracked at greater than 3 kts for more than one hour. The highest speeds were generally recorded between sunrise and noon just before sunset. None had speeds greater than 2 kts during the dark. The hours from midnight to dawn were usually the hours of least activity (Fig. 4).

Marlin SM87-8 was the least active (released

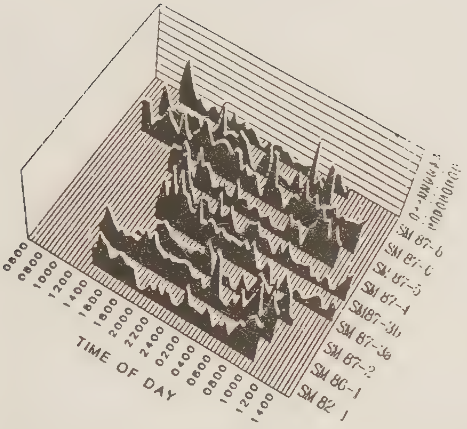

Figure 4. General activity pattern of eight striped marlin tracked for greater than 20 hours. The track of SM87-3 has been split into two 24-hour sections.

in fair condition) and spent nearly half of the tracking time at less than 1 kt and only 6% at greater than 2 kts. By contrast, marlin SM87-5, released in good condition, spent 40% of its time swimming in excess of 2 kts.

Depth preferences. Striped marlin off southern California are surface fishes, i.e., they spend all of their time in the upper, light-penetrating zone. This observation applies despite the fact that they are normally found only in the deep clear offshore waters, where the depth ranges between 400 and 2,000 m (1,300 and 12,000 ft). The greatest depth recorded by a marlin in our study was 93 m (305 ft). This was a short duration dive by SM87-3 and occurred just after sunset on the first tracking day. The second deepest dive was to 90 m (295 ft) by SM87-4. Like SM87-3, this dive occurred just after sunset and lasted only a few minutes.

Few marlin in our study descended to such depths. Marlins SM87-2, SM87-6, SM87-8 spent their entire tracking period in less than 40 m (131 ft). Four marlin (SM86-1, SM87-2, SM87-3 and SM87-5) spent their nighttime hours at significantly ($a = .01$, Kolmogorov-Smirnov) greater depths than their daytime hours. These fish modified their depths just after sunset. All four descended to depths approximately two to two-and-one half times their daytime depths. Marlin SM87-3 and SM87-5 returned to within 10 m of the surface at sunrise, but SM87-2 returned to near the surface at 0100 hrs and maintained that depth throughout the remainder of the tracking period. Marlin SM87-5 exhibited a pattern of extended deep dives during the hours of darkness that was not observed in the others. One particular dive to 70 m (230 ft) lasted 2.5 hours.

This pattern of descending to somewhat deeper depths during the nighttime hours has not been reported from other tracking studies and seems contrary to studies involving swordfish *(Xiphias gladius)* (Carey and Robison 1981), yellowfin tuna *(Thunnus albacares)* (Yonemori 1982), and skipjack tuna *(Katsuwonus pelamis)* (Yuen 1970). In these studies, the fish spent greater portions of time at depth during the day than at night.

Temperature preferences. Striped marlin are predominantly surface swimming fish and treat the thermocline break as a hindrance to vertical movements. Three of our marlin (SM82-1, SM87-6, and SM87-8) spent only 2.9% to 6% of their time below the thermocline. Others (SM87-3 and SM87-5) showed less reluctance to enter the cooler waters below the thermocline and spent from 25.3% to 76.7% of their time below the mixed layer. Dives from the mixed layer to below the steepest portion of the thermocline's temperature gradient were typically of short duration and quite abrupt. The coldest temperature reached was recorded by SM87-3 (also SM87-5) at 10°C (50%), although the time it spent in this 10°C water was less than 3 minutes. This fish spent about half of its 48-hour track in the mixed layer and half below it in water from 14 to 19°C (57 to 66°F). Of the daytime hours, 88% of the time was spent in the mixed layer, whereas only 9% of the nighttime was spent above the thermocline. Marlin SM87-4 spent more time below the mixed layer (76.6%) than any of the others. This was a particularly warm and sunny period and surface temperatures reached 22°C with a shallow 13 m thermocline. A total of 42.1% of the tracking period was spent at 16 to 19°C (61 to 66°F). Marlin SM87-5 spent 54% of its tracking time below the mixed layer. Four hours of this time was spent at temperatures between 10 and 12°C (50 to 54°F) indicating that striped marlin are capable of tolerating cold temperatures for extended periods.

There is, as discussed earlier, a difference between observed depth at night and that of the daytime. These marlin spent daylight hours at and near the surface with only short and infrequent excursions into and below the thermocline. During nighttime hours a greater amount of time was spent in and below the steepest part of the thermocline. Soon after sunset these fish descended to the thermocline and began making more numerous excursions between the surface and 50 to 70 m. They spent from 50% to 100% of the daytime in the mixed layer, compared to only 13% to 66% time at night. Two marlin, SM87-6 and SM87-8, spent 97% of the time in the mixed layer with no statistical difference between day and night. Temperature data for SM82-1 were insufficient for inclusion.

Sea-surface temperature. Satellite imagery of sea-surface temperatures was available for six of the marlin tracks. These photographs provide evidence of a strong surface temperature influence on horizontal movements of the fish. Just as the fish in this study showed a reluctance to spend much time in the colder water below the thermocline, they demonstrated an even greater preference for remaining in areas with warm surface waters. These photographs (Fig. 5), with the marlin tracks overlaid, illustrate a clear tendency for these fish to skirt around and avoid colder water masses. These marlin remained in water with 18.5 to 20°C (65 to 68°F) surface temperatures most of the time and tended to avoid a cooler body of water. Marlin SM87-3 spent its entire 48-hour track in the 20°C) water. Traveling northeast, SM87-5 encountered cooler water near the coast and turned southeast, traveling along the temperature break, and finally turned south and away from the colder water. SM87-6 moved north until reaching cooler water, where it turned northeast until it reached the cooler band of coastal water. It then turned south and then west to remain in the warm water. Although marlin SM87-4 spent

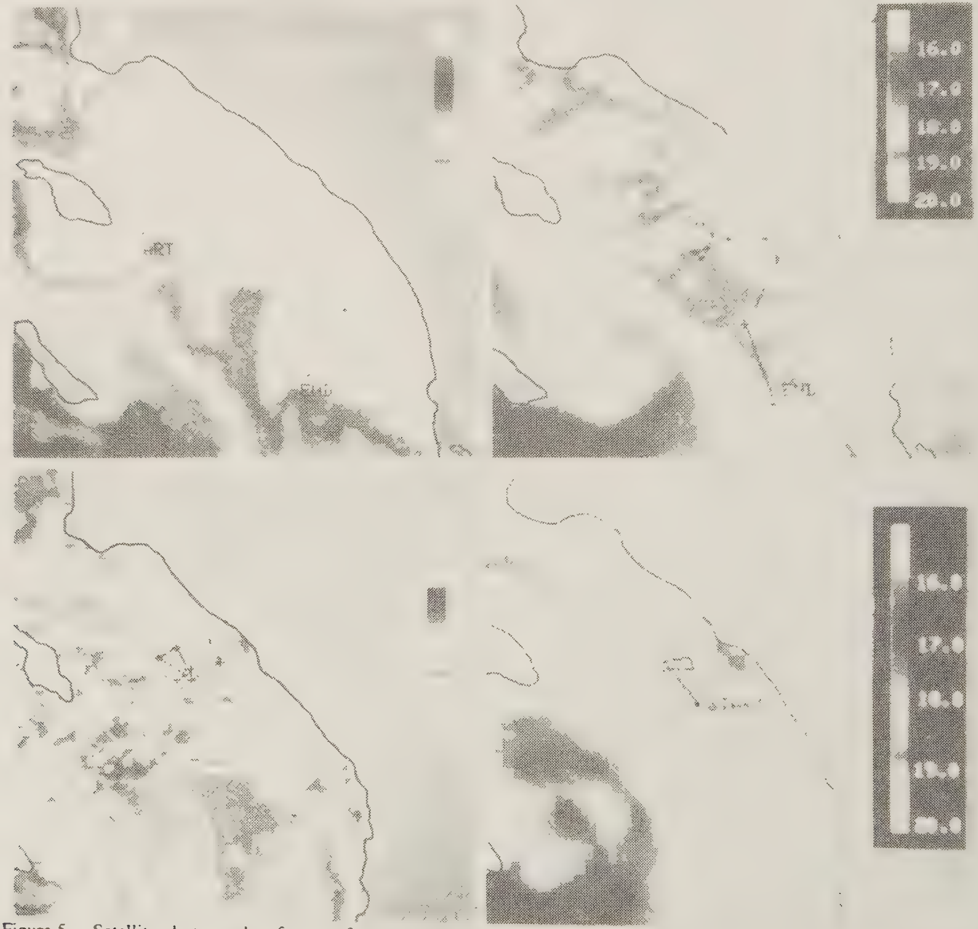

Figure 5. Satellite photographs of sea-surface temperatures with marlin track overlays provide good illustration of striped marlin presence in specific temperature zones.

76.7% of its time below the thermocline, it appeared to avoid the warm (22°C) water until near the end of the track. Here, it entered the warm coastal water and swam within 4 nm of the shore, an unusual occurrence for these largely offshore fish.

It is worthwhile mentioning that four of these marlin were lost soon after entering colder bodies of water, and that one (SM87-4) was lost shortly after entering a warmer surface water. None of these fish made a notable change in depth when entering a new body of water, but all changed their speed. Four slightly increased their speed while SM87-2 and SM87-4 slowed down as they entered water of different temperatures.

The photographs, taken from NOAA satellites on the occasion of each tracking cruise, were not available to us until after the actual cruise date. Thus, after reviewing these images, it is now apparent that several fish may have been lost as a result of sudden changes in course after encountering water masses of differing temperatures. The fish may have reversed direction in these cases, whereas we had assumed that the fading signal was due to the marlin outswimming the tracking vessel. In such a case, we may have increased our speed in the wrong direction.

Tagging Efficacy

We found the striped marlin to be a sturdy fish, tolerant of a great deal of handling. Eight of the twelve striped marlin were judged to be in good to excellent condition after they had been tagged and released. Three were listed as fair due to exhaustion. Although not injured, one (SM87-8) had everted its stomach in an attempt to regurgitate the baitfish and hook. It then re-swallowed it's stomach during capture and before tagging. This behavior is an apparently common method by which striped marlin attempt to expel undesired food items. This marlin was tracked for 24 hours, although it was the least active of the eight fish tracked.

During our cruises, we observed only two fish which died as a result of handling during capture. One of these was "tail-wrapped" and towed backwards for nearly an hour before being brought alongside. The other appeared to be in good condition when it was brought to the boat, but a failed attempt to plant a tag resulted in a 5-minute delay during which the fish was held by its bill against the fishing vessel's swim step. While struggling to free itself, it flailed against the swim step repeatedly, finally resulting in its death. Other fish, notably SM87-1, were held by their bills for 20 minutes before our arrival. Marlin SM87-1 appeared to be completely exhausted but not injured. It was subsequently tagged and tracked for 3.5 hours before an equipment failure resulted in our losing the fish.

Tagging-Induced Trauma

For a period of up to 2 hours following tagging and release, most fish displayed rapid changes in both heading and depth. Seven of the marlin descended to a deeper than normal depth and exhibited a heightened activity level immediately after release. Overall speed of travel varied between 2 and 3.5 kts and depths varied between 13 and 33 m (43 and 108 ft). These episodes lasted from 30 minutes to 2 hours, after which these marlin normally returned to near-surface waters. They then settled into swimming patterns which remained more consistent and generally more subdued for the remainder of the tracks. Three marlin did not exhibit a post-tagging pattern and stayed at 5 m or less for over an hour after release. Two moved moved away at 1 and 2 kts while the third (SM87-7) remained at the tagging site for about 2 hours.

We conclude that this initial burst of activity is a result of trauma induced during capture and tagging, and that the subsidence of this behavior, along with subsequent observations of feeding, sleeping, gathering into groups and "breezing," are good indications that this trauma is quickly overcome.

Summary

During September, 1982, a striped marlin was tagged with a sonic transmitter and tracked by National Marine Fisheries Service (NMFS) biologists, in waters off southern California. This event was the first time this species had ever been tracked. In 1986 and 1987, 11 more striped marlin were tagged with sonic transmitters, also off southern California. This renewed effort was conducted as a joint program of the National Marine Fisheries Service and the California Department of Fish and Game. Eight marlin were successfully followed for periods ranging from 20 to 48 hours and covered 254 nautical miles.

No single repetitive behavior was found to be characteristic of all the marlin tracked during this study, although a few behaviors were common to several fish. The behaviors were classified

into three broad categories including occasional behaviors, periodic behaviors, and those influenced by environmental parameters.

Two patterns of horizontal movement emerged from these tracks. Five of the eight moved predominantly in one direction after tagging, usually south. The other 3 marlin remained in the vicinity where they were first captured. Distances traveled ranged from 22 to 57 nautical miles at an average speed of 1.18 kts.

The greatest activity was observed during the late afternoons, when some of the marlin swam rapidly down-wind and down-swell in a behavior known to fishermen as "tailing" or "breezing". General activity of all fish slowed during the night. Several fish exhibited behavior which might be characterized as "sleeping", the fish remaining motionless, just below the surface, for 1 to 4 hours. This behavior was observed only during the night and early morning hours. Vertical movements during day and night hours showed some consistency among all marlin tracked. These striped marlin showed a preference for warm surface water and remained within the mixed layer more than 85% of the time. Four fish spent their nighttime hours at somewhat greater depths than during the daytime.

Vertical movement tended to be exaggerated and erratic for up to 2 hours after tagging. Beyond this time, the fish assumed a behavioral pattern which remained consistent throughout the duration of the track. We believe that this pattern indicates that the trauma induced by capture and tagging is short lived and tracks of as little as 24 hours should faithfully reflect "normal" marlin behavior.

Acknowledgments

Special thanks to Earl Weber, whose personal contributions to the development of this project made the whole thing happen, and to Rich Johnson, for donating his time and vessel, the *Marie B* for the work in 1982. Also thanks to Gerald Thompson, managing owner of the *Pacific Clipper*, and to Ron O'Rona, the skipper, who lost a lot of sleep during some long nights of tracking. We wish to thank the National Coalition for Marine Conservation-Pacific Region, the Los Angeles Billfish Club, the San Diego Marlin Club, and the Dana Angling Club for their support, and to all the anglers who donated their marlin to our research. Rich Brill and the NMFS staff decoded depth data for several tracks. Norman Bartoo, Rick Klingbeil, Jean Davis, and Gary Sakagawa reviewed the manuscript; Ken Raymond, Roy Allen, and Henry Orr prepared the figures.

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*use of trade names does not indicate endorsement by the NMFS or CDFG.

Literature Cited

Bedford, D.W. and F. Hagerman. 1983. The billfish fishery resource of the California current. CalCOFI Rep. XIV:70-78.

Bedford, D.W. 1987, Shark management: A case history — The California pelagic shark and swordfish fishery. Proceedings of the Sea Grant Conference on Sharks, Portland, Oregon, 1985: 161-171.

Carey, F.G. and R.J. Olson. 1981. Sonic tracking experiments with tunas. ICCAT, Collective Volume of Scientific Papers 17(2):458-466.

Carey, F.G. and B.H. Robinson. 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. Fishery Bulletin 79(2):277-292.

Eldridge, M.B. and P.G. Wares. 1974. Biological Observations of billfish taken in the eastern Pacific Ocean 1967-1970. *In:* R. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium Kailua-Kona, Hawaii, 9-12 August 1972. U.S. Dept. Commerce, NOAA TR NMFS SSRF-675:89-101.

Holland, K., R. Brill, S. Furguson, R. Chang, and R. Yost. 1986. A small vessel technique for tracking pelagic fish. Marine Fisheries Review 47(4):26-32.

Squire, J.L., Jr. 1987a. Pacific billfish angler catch rates for key area stock assessments. Marine Fisheries Review 49(2):15-25.

Squire, J.L., Jr. 1987b. Striped marlin migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program: Its relation to resource management. Marine Fisheries Review 49(2):26-43.

Squire, J.L., Jr. and D.W.K. Au. 1989. Management of Striped Marlin *(Tetrapturus audax)* Resources in the Northeast Pacific — A Case for Local Depletion and Core Area Management. Current volume.

Yonemori, T. 1982. Study of tuna behavior, particularly their swimming depths, by the use of sonic tags. Translated from: Enyo (Far Seas) Fisheries Research Laboratory, Shimizu, Newsletter No. 44 (April):1-5.

Yuen, H.S.H. 1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Bd. Canada 27(11):2071-2079.

Yuen, H.S.H., A.E. Dizon, and J.H. Uchiyami. 1974. Notes on the tracking of the Pacific blue marlin, *Makaira nigricans*. *In:* R.S. Shomura and F. Williams (eds.), Proceedings of the International Billfish Symposium. Kailua-Kona, Hawaii. August 1972, Part 2. Review and Contributed Papers: 265-268. U.S. Dept. Commerce, NOAA Tech. Rep. NMFS SSRF-657.

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Statistical Aspects of Fishery Papers

In two papers that follow, the authors address statistical problems that they have perceived in published fishery research papers. The theme of the larger meeting that included our symposium was that fishery science is multidisciplinary. No fishery scientist can be expected to be expert in all the fields represented in the science. This is particularly true in regard to statistical and mathematical skills, which some have in abundance but others lack. Those who do not possess such skills should seek statistical and mathematical help in the preparation of their papers—but carefully, because miscommunication between a consultant and a consultee with disparate skills is frequent.

Editors are aware of and concerned about these problems. No editor wishes to publish a paper that is incomplete or in error. How the statistical quality of papers in fishery journals could be improved was the subject of some discussion during the symposium. Some of the suggestions made were (1) to provide more statistical training in fishery programs, (2) for editors to use as reviewers the younger, statistically trained members of the profession, and (3) for the journal to hire a statistical reviewer. The first of these suggestions will only be beneficial in the long term. To set the second of these in motion, editors need to work with academic institutions to develop a list of statistically trained persons. The third involves costs that must be considered. Alternatively, when the editor and referee are in doubt as to the quality of the analyses performed, the author could be requested to have the work certified by an expert in the appropriate quantitative field. This might require the author or the author's organization to pay a fee to the certifying expert. The certification, including the name of the person involved, would be included as a footnote. As a variant of this, the quantitative expert might be listed as a coauthor. Some recent experiences with medical publications, in which long lists of authors are common, show that some coauthors may not take seriously their responsibilities for the quality or accuracy of the paper. Thus, having a quantitative expert listed as a coauthor may not fully reassure the editor.

It is unlikely that a single solution will resolve all such problems. Each editor must determine what seems best, taking into account the needs and scientific level of the journal, the fraction of statistical or mathematical content of the papers submitted, and the budget. Editors probably should seek a candid evaluation of recently published papers to determine if this is a serious problem for their journal. In any case, editors need to seriously consider this problem and perhaps emphasize it in communications with the associate editors and reviewers.

JOHN HUNTER
Editor

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BATHYMETRIC PATTERNS IN SIZE, AGE, SEXUAL MATURITY, WATER CONTENT, AND CALORIC DENSITY OF DOVER SOLE, *MICROSTOMUS PACIFICUS*

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ABSTRACT

Ninety-eight percent of the spawning biomass of Dover sole, *Microstomus pacificus*, in central California waters live in a region of the continental slope between 640 and 1006 m (350-550 fath.) characterized by low oxygen concentrations (0.27-0.36 ml/l) and cold temperatures (5.9°C-3.2°C). Juvenile Dover sole settle on the continental shelf and gradually move down the slope over their lifetime, reaching the oxygen minimum zone as they become sexually mature. Fifty percent of Dover sole in central California reach sexual maturity when about 31 cm long and about seven years of age. The ontogenetic movement down the slope continues after sexual maturity and is accompanied by a marked increase in water content of the body and a consequent decrease in caloric density per gram wet weight. For example, caloric density decreases from about 0.86 kcal per gram wet weight[1] (83% water) for 275-mm fish living at 200-400 m, to 0.60 kcal per gram wet weight (90% water) for a fish 440 mm long living at about 900 m. Female Dover sole may live as long as 53 years, and males 58 years. Water content appears to be a function of age as well as length and depth.

RESUMEN

El 98% de la biomasa del desove del lenguado de las aguas de California central, *Microstomus pacificus*, vive en un área del talud continental entre los 640 y los 1006 m caracterizada por bajas concentraciones de oxígeno (0.27–0.36 mL/L) y bajas temperaturas (5.9°C–3.2°C). Los juveniles se establecen en la plataforma continental y gradualmente, durante su desarrollo, se van moviendo hacia el talud y a lo largo de él, llegando a la zona de mínimo oxígeno cuando alcanzan la madurez sexual. El 50% del lenguado alcanza la madurez sexual cuando mide aproximadamente 31 cm de longitud, a los 7 años de edad. El movimiento descendiente a lo largo del talud durante la ontogénesis continúa pasada la madurez sexual, y es acompañado por un incremento marcado en el contenido de agua del cuerpo y consequentemente, por un decrecimiento en la densidad calórica por gramo de peso húmedo. Por ejemplo, la densidad calórica de un pez que mide 275 mm y vive a 200–400 m de profundidad decrece de 86 kcal por gramo de peso húmedo (83% de agua) a 60.3 kcal (90% de agua) para un pez que mide 440 mm de longitud y vive a 900 m de profundidad. Las hembras pueden vivir hasta proximadamente los 53 años de edad y los machos hasta los 58. El contenido de agua parece estar relacionado con la edad y el largo del individuo y con la profundidad a la cual vive.

INTRODUCTION

Dover sole, *Microstomus pacificus*, are found from the Aleutian Islands in the Bering Sea to Baja California (Eschmeyer et al. 1983). The U.S. fishery for Dover sole occurs from Point Conception, California, to the Canadian border. Dover sole inhabit depths ranging from about 55 to 1300 m. Older and larger fish usually occur in the deeper portion of the depth range, and younger and smaller fish in the shallower depths. A seasonal inshore migration has been described: fish move into deep water in the fall before the spawning season and into shallow water in the summer (Hagerman 1952; Alverson 1960; Pearcy et al. 1977). Most individuals apparently remain in the same general locality throughout their lives. Although longshore movements of up to 360 mi (579 km) in seven years have been recorded, 97% of tagged individuals were recaptured within 50 km of where they were tagged (Westrheim and Morgan 1963).

Large Dover sole from deep water are often "jellied" (have flesh with an unusually high water content). This "jellied" consistency limits the market value of fillets from large Dover sole because their desirability is reduced (Hendricksen et al. 1986). Owing to the ontogenetic migration into greater depths, and the extensive depth range, the demographic and physiological characteristics of Dover sole change strikingly with depth, age, and length. Thus neither the dynamics nor the ecology of Dover sole populations can be properly analyzed or understood without a careful evaluation of the relation between depth and key physiological and population variables.

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[1] **Calories per gram wet weight have been corrected from original publication by a factor of 10^{-2}.**

The objective of this paper is to describe the relationships between depth, length, age, sexual maturity, water content, caloric density, and biomass of Dover sole. We also provide data on the temperature and oxygen content of the habitat in which fish of different length and age are found. Our analysis does not include data for the summer months, when fish may have a shallower distribution (Alverson 1960).

METHODS

Sea Collections

Research trawl collections were taken at depths between 69 and 1394 m (38–762 fath.) off the central California coast between Point Conception and Half Moon Bay, California, during 1985–88 by NOAA-Southwest Fisheries Center (SWFC) personnel (table 1). Trawl collections were opportunistic before 1987. In 1987, samples were taken at 183-m (100-fath.) intervals along transect lines; in 1988 a random sampling design stratified by depth was used (figure 1).

In all years fish were sexed and measured for total length. Before January 1987, fish were randomly sampled from each collection until 25 females had been identified and their ovaries preserved for later assessment of maturity; the females and some males were frozen for subsequent extraction of otoliths and determination of water content as described below. During January–February 1987, either all of the Dover sole in the trawl collection or 100 fish were randomly sampled, and 25 females were assessed for gonad maturation. Four to six fish of each sex were weighed and frozen for later removal of otoliths and tissue for analysis of water content. The bottom temperature (reversing thermometer on Nansen bottle) and oxygen content (Winkler titration) were measured for 17 Nansen cast stations ranging from 183 to 1,280 m (100–700 fath.; figure 1, left, triangles). The total trawl catch of Dover sole was weighed during 1987 and 1988. In 1988, up to 100 Dover sole were randomly sampled and weighed by sex; the maturation state of all ovaries was determined.

Age Determination

Ages were determined from otoliths removed from 341 females and 64 males captured during 1985–86 and from 154 females and 97 males captured in 1987. Left otoliths were embedded in epoxy resin and cut with a diamond wafering blade in a thin cross section through the nucleus from dorsal to ventral (Chilton and Beamish 1982). Thin sections were mounted on microscope slides with Eukitt mounting medium, polished, and read with a compound microscope. A typical otolith section is shown in figure 2. Counting procedures followed those of Chilton and Beamish (1982). Each otolith was read independently by three observers without knowledge of the length of the fish. Otoliths whose readings differed by more than 10% among the readers were reread using the same protocol until the readings agreed to within 10%. Estimated age was the average of the individual readings. Parameters of the von Bertalanffy equation relating length and age were estimated by the simplex method (O'Neill 1971).

TABLE 1
Sources and Numbers of Dover Sole Used for Analyses

		Number of positive trawl collections			Number of Dover sole used in various analyses					
			Depth							
Dates	Sampling type[a]	*N*	Min	Max	Percent water	Calories	Age	Size at depth	Sexual maturity	Oxygen and temperature
12/3–12/12/85	OP	11	94	704	108	7	37	195	104	—
1/14–2/24/86	PS	2	330	600	115	—	180	—	—	—
3/5–3/7/86	OP	8	52	500	165	18	14	210	—	—
5/2–5/4/86	OP	3	175	537	60	2	62	74	—	—
1/11–2/15/87	LT	49	99	705	265	—	255	3225	—	17[b]
2/23–4/9/88	SR	51	38	602	—	—	—	2800	—	—
		Total specimens			713	27	548	6504	104	—

[a] OP = opportunistic trawl samples; PS = port samples; LT = line-transect trawl samples; SR = stratified random trawl samples.
[b] Number of Nansen cast stations.

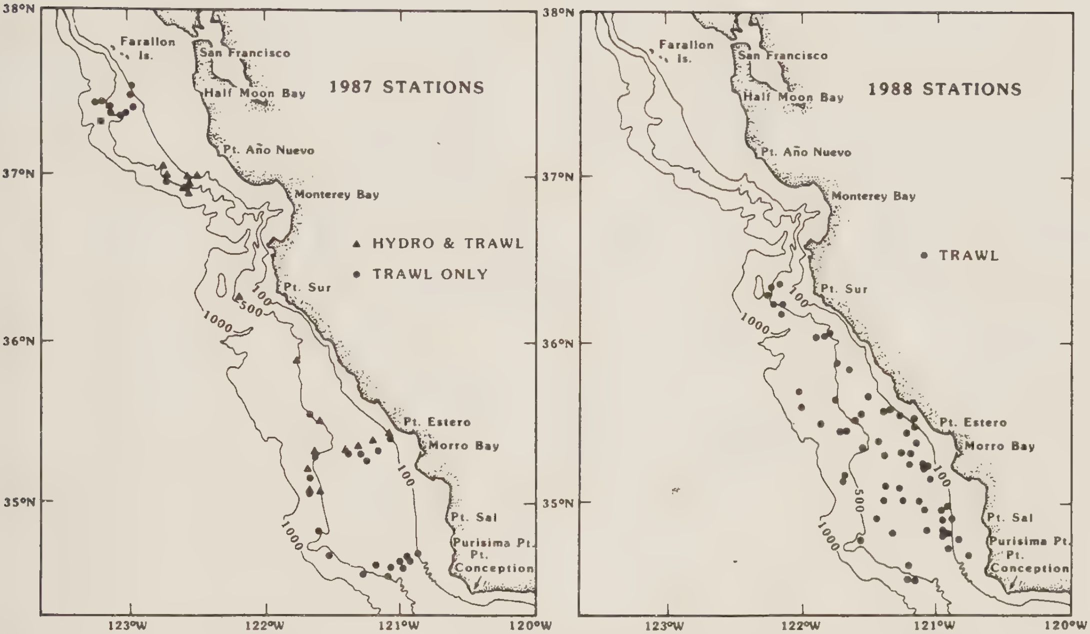
38°N
37°N
36°N
35°N
Farallon Is.
San Francisco
Half Moon Bay
1987 STATIONS
Pt. Año Nuevo
Monterey Bay
▲ HYDRO & TRAWL
● TRAWL ONLY
Pt. Sur
100
500
1000
Pt. Estero
Morro Bay
Pt. Sal
Purisima Pt.
Pt. Conception
123°W
122°W
121°W
120°W
1988 STATIONS
● TRAWL

Figure 1. *Left*, trawl stations occupied on the January–February 1987 groundfish cruise of the R/V *David Starr Jordan*. *Right*, trawl stations occupied on the February–March 1988 groundfish cruise of the R/V *David Starr Jordan*.

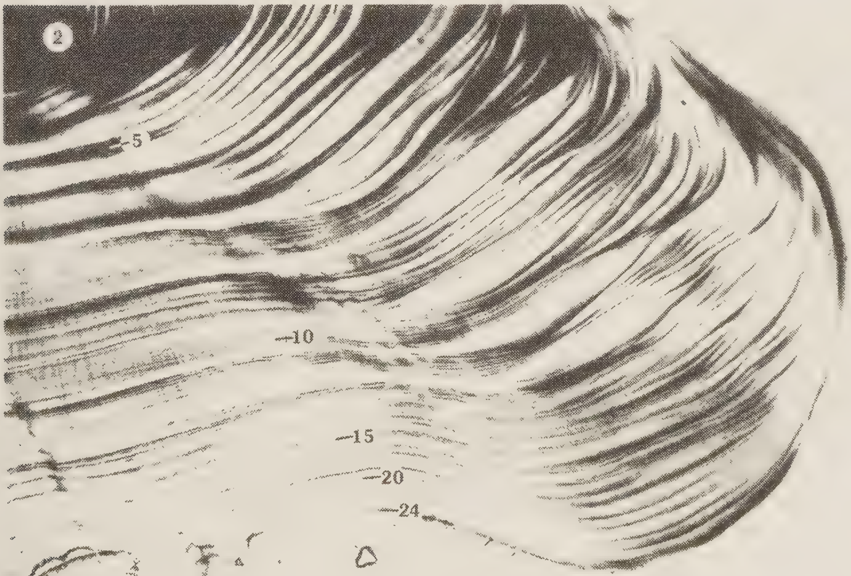
2
5
10
15
20
24

Figure 2. Thin section of the left otolith of a 24-year-old Dover sole. Numbers indicate years.

Biomass

We used the mean biomass in the area swept by trawls, and total area within three depth strata to estimate Dover sole biomass. The survey area extended from 34°30′N, 120°30′W to 36°30′N, 122°30′W (Butler et al. 1989).

Sexual Maturity

The size at first maturity of females taken in December 1985 was estimated by logistic regression analysis (Draper and Smith 1981; Engelman 1988). Data from the other surveys (table 1) were not appropriate for estimating sexual maturity because the spawning season began before the first survey. The possibility of mistaking immature ovaries for postspawning ovaries was minimized because December appears to be early in the spawning season (Hunter, unpublished data). Ovaries with yolked oocytes were considered to be mature, and those without yolked oocytes to be immature.

Water Content

We measured water content by determining the wet weight of a tissue sample (about 3.5 g) and then drying it to constant weight at 60°C. The white muscle samples were taken from the right side of the fish between the lateral line and the dorsal fin at the insertion of dorsal rays 30 to 36, and the red muscle samples were taken from the right side above the lateral line and behind the eye.

To determine whether a single tissue sample represented water content of the whole fish, we measured the entire water content of 20 females, 6 males, and one fish of indeterminate sex by grinding and drying the entire fish after removing red and white muscle tissue samples from the locations described above. We then regressed water content (in percent of wet weight) of the entire fish (H) on tissue sample water content (figure 3):

$$H = -5.08 + 1.05\,h_1, \qquad (1)$$

where h_1 is water content of white muscle ($r^2 = 0.906$, $n = 27$; $p < 0.01$). The slope of this equation did not significantly differ from 1.0, nor did the intercept differ from 0. On the basis of these results we assumed that the percentage of water in the white muscle tissue samples was the same as that of the whole fish. Whole fish water content was estimated (equation 1) from white muscle tissue samples collected at sea for 106 fish collected in 1985, 335 fish collected in 1986 (90% females), and 265 fish (males and females) collected in 1987.

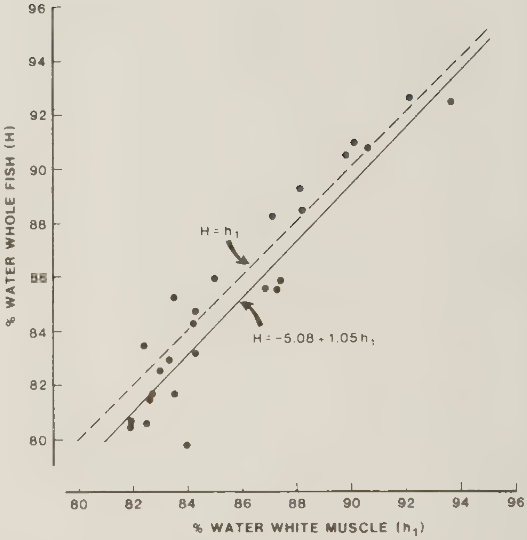

Figure 3. Relation of water content of whole Dover sole to water content of white muscle. *Solid line* is regression line fit to data; *dashed line* is one-to-one relationship.

Water content of the red muscle tissue sample was also linearly related to water content of the entire fish, although the relationship was poorer than that for white muscle:

$$H = -51.1 + 1.62\,h_2, \qquad (2)$$

where h_2 is water content of red muscle ($r^2 = 0.837$, $n = 27$; $p < 0.01$).

Caloric Density and Fat Content

To determine caloric density (kcal/gm) of entire fish for 26 Dover sole, we used a Parr bomb calorimeter and standard techniques (Parr Instrument Co. 1960; Paine 1971). The values reported here are the means of three determinations. Fish were selected by size to obtain caloric measurements over a wide range of water content (the fish sampled ranged from 80% to 94% water).

To determine fat content we used a Soxhlet extraction with 2:1 chloroform-methanol. This technique did not provide an accurate estimate of total fat content because the extraction period (48–72 hrs) was too short for fish with a high fat content, such as Dover sole. Notwithstanding this bias and other problems associated with chloroform-methanol extractions (Dobush et al. 1985), we believe that the data provided useful information about fat concentration.

RESULTS

Length and Depth

The mean length of Dover sole increases rapidly with depth over the first 300 fath. (549 m) and thereafter more slowly. The relationship between depth and size of Dover sole varied little among years (figure 4, top and middle). The combined data for all surveys clearly indicate that males taken at a given depth are smaller than females (figure 4, bottom).

Age and Growth

Male and female Dover sole differ in size at age (figure 5). Estimates from counts of annuli in thin sections of otoliths indicate that the fish live long lives. The maximum estimated age was 56 years for a 460-mm male and 51 years for a 492-mm female.

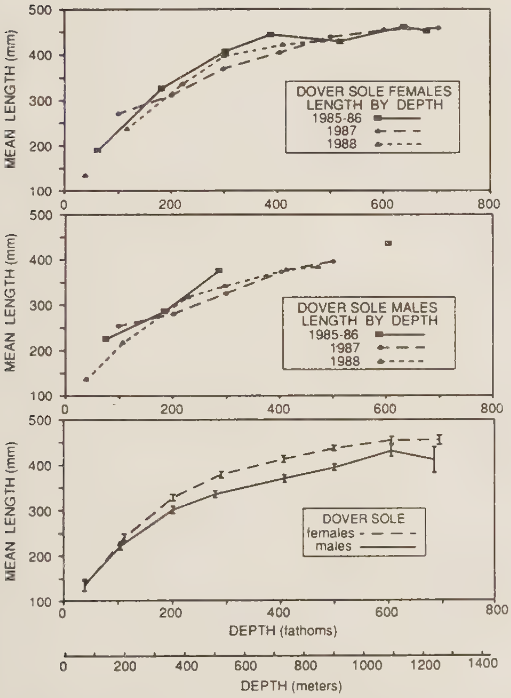

Figure 4. Mean length of Dover sole collected at different depths. *Top*, females; *middle*, males; *bottom*, all years combined with ± 2 SE

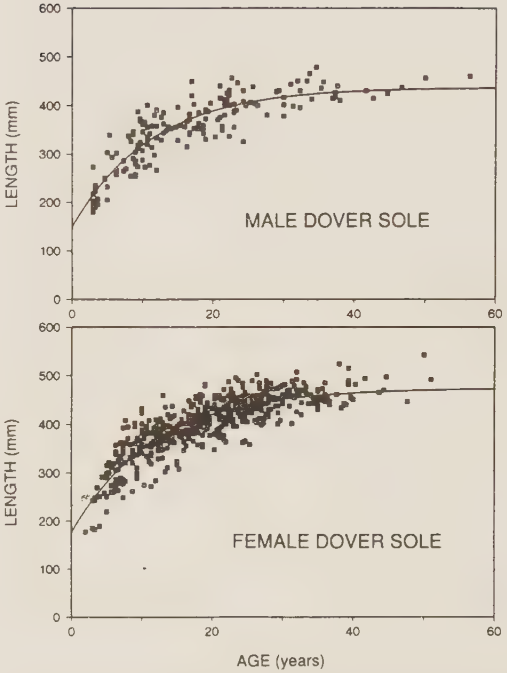

Figure 5. *Top*, length and age (calculated from otolith section) of male Dover sole. *Solid line* is von Bertalanffy curve with L_∞ = 437 mm, growth parameter K = 0.089, and t_0 = −4.7 yr. *Bottom*, length and age (calculated from otolith section) of female Dover sole. *Solid line* is von Bertalanffy curve with L_∞ = 474 mm, growth parameter K = 0.085, and t_0 = −5.5 yr. See text for equation 3.

Parameters of the von Bertalanffy growth model,

$$L_t = L_\infty (1 - e^{-K(t-t_0)}), \qquad (3)$$

were L_∞ = 437 mm, K = 0.089, and t_0 = −4.7 years (n = 161, $p < 0.01$) for male Dover sole. Estimates of parameters for females were L_∞ = 474 mm, K = 0.085, and t_0 = −5.5 years (n = 495, $p < 0.01$). Male and female Dover sole longer than 40.0 cm may be any age from 8 years to 40 or 50 years. Neither our methodology nor any other has been validated for Dover sole. Nevertheless, we believe our age estimates approximate the true age, because the otolith section method has been validated for another species in the same habitat (*Anoplopoma fimbria*; Chilton and Beamish 1982).

Our age estimates are much greater than those obtained from scales (Demory 1972; Mearns and Harris 1975). However, tag-and-recapture studies

(Pikitch and Demory 1988) have shown that scales underestimate the age of Dover sole. The maximum age observed in this study (56 years) is in agreement with the longevity that Pikitch and Demory (1988) predicted from tag-and-recapture studies and errors in scale readings. A significant fraction (40%) of females in our samples were older than 20 years. Our results suggest that estimates of the productivity of Dover sole stocks based on ages estimated from scales may be seriously flawed.

Water Content

Data for females taken from December 1985 through May 1986 indicate that the mean water content of white muscle remains constant at about 82% in 15–30-cm females but increases with length in larger Dover sole to about 90% in 50-cm females (figure 6). The concentration of water in the red muscle followed a similar trend, but the increase in water content with length was much less. Average water content of red muscle in 50-cm females was only 85%. These data indicate that red muscle is conserved. The red muscle in the anterior upper trunk region of the eyed side of the body is the largest concentration of red muscle in the body and is probably used to control head movements during feeding. The color of the red muscle changed with fish length. Larger fish had darker red muscle, indicating that the myoglobin content of the muscle may be higher in larger fish.

The mean water content of males taken in January–February 1987 did not differ from that of females from that sample within the same 5-cm length class (ANOVA for five 5-cm length classes, 254–324 to 475–524 mm, per sex where $p = 0.90$; figure 7). The water content of Dover sole (both male and female) as a function of length showed little variation between years; the data for December 1985–May 1986 were essentially the same as those for January–February 1987 (figure 7). Combining data for all years and sexes indicates that the average water content for fish less than 275 mm was constant at 82.9% ($n = 90$, SD = 1.00), and for fish greater than 275 mm it increased with length (L) according to the equation

$$H = 72.7 + 0.036\,L \tag{4}$$

($r^2 = 0.58$, $n = 506$; $p < 0.01$).

Water Content, Age, Length, and Depth

In the previous sections we showed that water content increases with fish length and that length increases with depth and age. In this section we describe the relationships between water content, length, depth, and age of Dover sole females. A

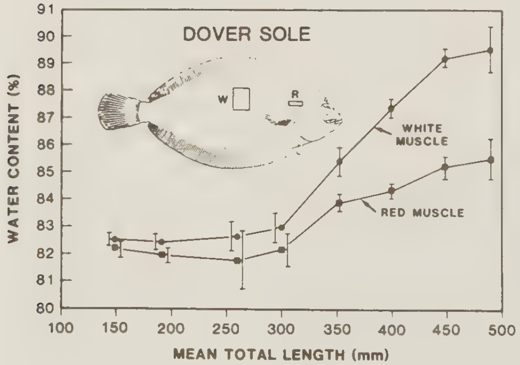

Figure 6. Water content in white and red muscle versus total length of female Dover sole. Insert shows locations of tissue samples—W for white muscle and R for red muscle.

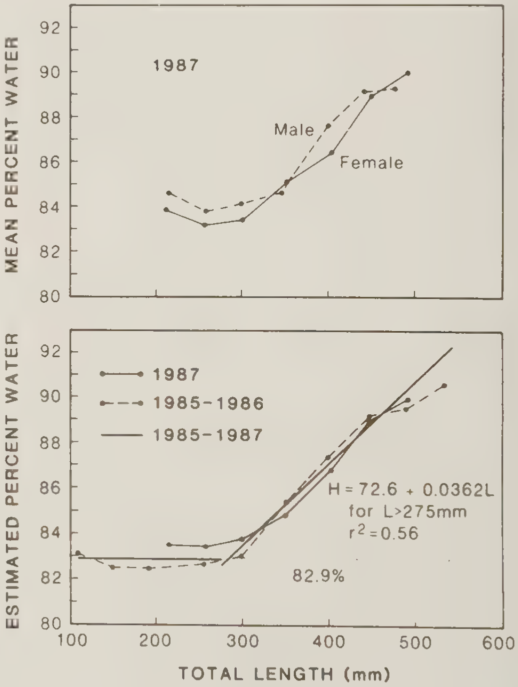

Figure 7. *Top*, water content of white muscle versus total length of female (N = 163) and male (N = 98) collected in 1987. *Bottom*, water content in white muscle of both sexes for 1985–86 (*dashed line*), 1987 (*thin line*), and 1985–87 (*thick line*).

stepwise multiple regression analysis indicated that all three independent variables (age, length, and depth) accounted for significant variation in the dependent variable, water content: the coefficient for age was the first selected (table 2). The final equation was

$$H = 78.7 + 0.1226\ T + 0.0123\ L + 0.0026\ D \quad (5)$$

where H is water content (percent of wet weight), T is age (years), L is length (mm), and D is depth (fath.) ($R^2 = 0.69$, $n = 519$; $p < 0.01$). Biological interpretation of the significance of the individual regression coefficients in this equation could be misleading (Sokal and Rohlf 1981) because, as is indicated in the correlation matrix (table 2), all the variables are correlated with each other; length is correlated with age and depth as well as water content.

Caloric Density

Caloric density (kcal per g ash-free dry weight) was correlated with fat concentration (F, in percent of dry weight). This relationship was less precise ($r^2 = 0.57$, $n = 26$; $p < 0.01$) than one would expect on physiological grounds because of our failure to extract all the lipids in some of the fish. Nevertheless, figure 8 clearly indicates that caloric density and fat concentration are linked, as would be expected.

No significant relationship existed between caloric density and water content. There was no apparent relationship between fat concentration and water content ($r^2 = 0.02$) when length was not included as a variable. When length (L) was included as an additional third dependent variable in a stepwise multiple regression analysis (table 3), a definite relationship existed between caloric density (C_d) and

TABLE 2

Analysis of the Relation Between Water Content (*H*) of Dover Sole and Their Age (*T*), Length (*L*), and Depth (*D*)

Stepwise regression

Step	1	2	3
Constant	82.63	78.31	78.71
Age (*T*)	0.2213	0.1272	0.1226
t-ratio[a]	28.28	10.94	10.69
Length (*L*)		0.0157	0.0123
t-ratio		10.25	7.30
Depth (*D*)			0.00260
t-ratio			4.61
S	1.82	1.66	1.63
R^2	60.73	67.37	68.62

Analysis of variance

Source	DF	SS	MS	*F*	*p*
Regression	3	2,981.00	993.67	375.31	<0.0005
Error	515	1,363.52	2.65		
Total	518	4,344.52			

Source	DF	Seq SS
Age (*T*)	1	2,638.47
Length (*L*)	1	288.64
Depth (*D*)	1	53.89

Matrix of correlation coefficients

	Water (*H*)	Age (*T*)	Length (*L*)
Age	0.779		
Length	0.773	0.789	
Depth	0.626	0.578	0.682

[a] For $p = 0.05$, the t-ratio is 1.96.

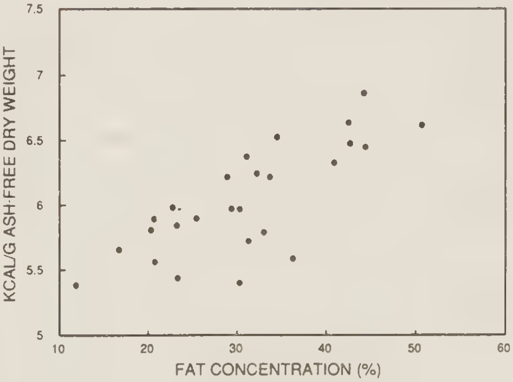

Figure 8. Caloric density versus fat concentration in Dover sole.

TABLE 3

Analysis of Variance Stepwise Regression of the Caloric Density of Dover Sole (C_d, kcal/g ash-free dry weight) on Their Total Length (*L*, in mm) and Water Content (*H*, in Percent)

Summary

Step	1	2
Constant	8.755	13.540
Water (*H*)	−0.032	−0.104
t-ratio[a]	−1.65	−5.86
Length (*L*)		0.0042
t-ratio		5.76
S	402	263
R^2	10.21	63.22

Analysis of variance

Source	DF	SS	MS	*F*	*p*
Regression	2	2.725	1.363	19.76	<0.0005
Error	23	1.586	0.069		
Total	25	4.311			

Source	DF	Seq SS
L	1	0.358
H	1	2.367

[a] For $p = 0.05$, the t-ratio is 2.07.

water content of white muscle (H, in percent wet weight) yielding the equation

$$C_d = 13.540 + 0.0042\,L - 0.1044\,H \qquad (6)$$

with $R^2 = 0.60$, $n = 26$; $p < 0.01$ (figure 9). To further evaluate these data we analyzed covariance by arranging the data into three length classes (114–296 mm, 303–396 mm, and 408–506 mm) and regressed water content on calories within length class. This analysis indicated that the relationship between calories and water content differed significantly among the three length classes (233, 350, and 453 mm mean total length; $p < 0.01$). For the overall mean water content (85.6%), the adjusted mean kcal per g ash-free dry weight are 5.634 at 233 mm, 6.078 at 350 mm, and 6.424 at 453 mm. The relationship between caloric density and length was not significant ($r^2 = 0.037$, $n = 27$; $p = 0.169$). Thus, the relationship between caloric density and water content changes with length.

The relationship between length, water content, and caloric density in terms of wet weight (C_w) was also evaluated. The multiple regression equation was

$$C_w = 651 + 0.0742\,L - 7.06\,H \qquad (7)$$

where C_w = kcal per 100 g wet weight, L = length, and H = water content of white muscle ($R^2 = 0.98$, $n = 26$; $p < 0.001$). R^2 is high because the water content of the fish largely determines the caloric density when it is expressed on the basis of wet weight.

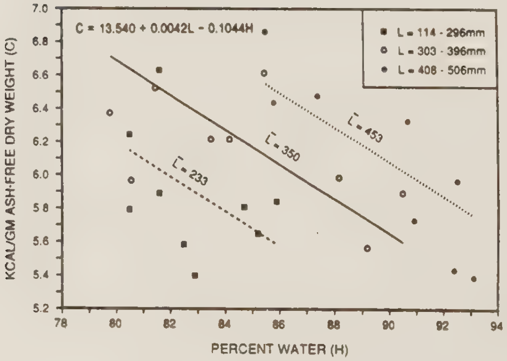

Figure 9. Caloric density and water content of Dover sole in three size classes. (See equation 6 in text for multiple regression relation of caloric density with length and water content.)

We also wished to examine how calorie content varied with depth. We used the multiple regression equation 6 to compute the caloric density (C, in kcal per g ash-free dry weight) of female Dover sole as a function of length and water content. We grouped the estimated caloric densities into seven 100-fath. (183-m) depth classes and calculated a mean and standard deviation (SD) for each class; the SD includes the variance associated with equation 6 (Draper and Smith 1981; figure 10, top).

A significant difference existed between the mean caloric density of females in the 100-fath. depth class and those in all other depth classes combined ($t = -7.34$, d.f. = 37.7, $p < 0.001$; d.f. was computed from the formula given by Zar [1984]). The mean caloric density for females taken in the 100-fath. depth class was 5.761 kcal per g ash-free dry weight ($n = 34$, SD = 292) and that of females taken at

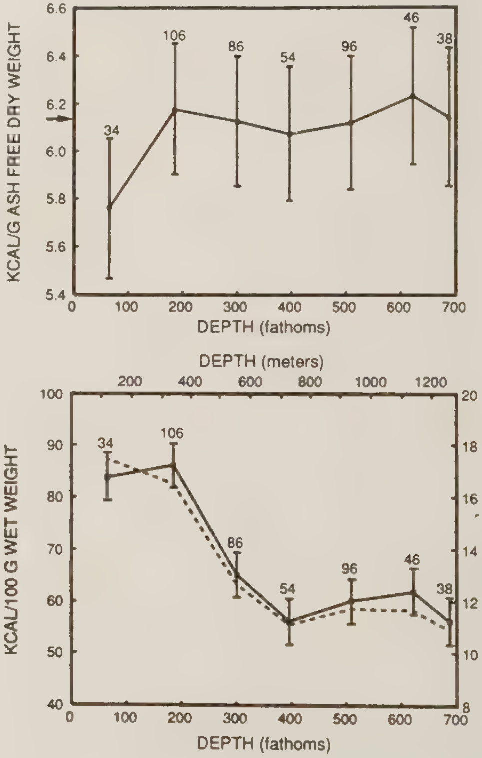

Figure 10. *Top*, kcal per g ash-free dry weight, SD and *N* within 100-fath. depth classes. Arrow is mean caloric density for depths ≥150 fath. *Bottom*, kcal per 100 g wet weight (*left axis*) and the complement of water content (*right axis*) within 100-fath. depth classes.

depths greater than 150 fath. was 6.141 kcal (n = 426, SD = 272). Thus, the Dover sole living in shallow water (50–150 fath.; 91–274 m) have a lower caloric density per unit dry weight than Dover sole living at greater depths.

A different pattern in the change in caloric density with depth occurs if caloric density is expressed in terms of wet weight rather than dry. Using the same data and equation 7, we recalculated the average caloric density of females on a wet-weight basis per depth class. On a wet-weight basis, the caloric density (kcal per g wet weight) declines with depth because of the increase in water content (figure 10, bottom). As would be expected, the decrease with depth in caloric density of Dover sole wet weight mimics the decline in the complement of the water content (100 − percent water; figure 10).

These measurements were made during the period in which Dover sole mature sexually and begin to spawn (December–February). Other patterns may exist at other times of the year.

Sexual Maturity

The sexual maturity of Dover sole females was estimated by calculating the fraction mature (M) for each of seven 50-mm length classes (255–526 mm). These data were fit by maximum likelihood estimates of the parameters to a logistic model

$$M = \frac{e^{a-bx}}{1 + e^{a-bx}} \tag{8}$$

where $a = -9.947$, standard error (SE) of a = 0.00688, and t = 4.657 (d.f. = 102, $p < 0.01$); b = 0.0320, SE of b = 2.159, and $t = -4.608$ (d.f. = 102, $p < 0.01$); and n = 104. This equation predicts that 50% of Dover sole females of 311-mm length are mature (figure 11). The smallest Dover sole with advanced yolked oocytes in our collections was 290 mm long. Judging from our age-length relation for female Dover sole (equation 3), a length of 311 mm corresponds to an age of about 7 years, and a length of 290 mm corresponds to about 6 years.

The mean lengths per depth class were used to calculate how sexual maturity varied with depth. Mean female lengths were computed for each of eight 100-fath. (183-m) depth classes (all trawl data, 1985–88; n = 4,412; table 1; figure 4), and the maturity was calculated using equation 8. This analysis indicated that sexual maturity increased with depth from about 60% at 200 fath. to 90% or more at depths of 300 fath. (549 m) or greater.

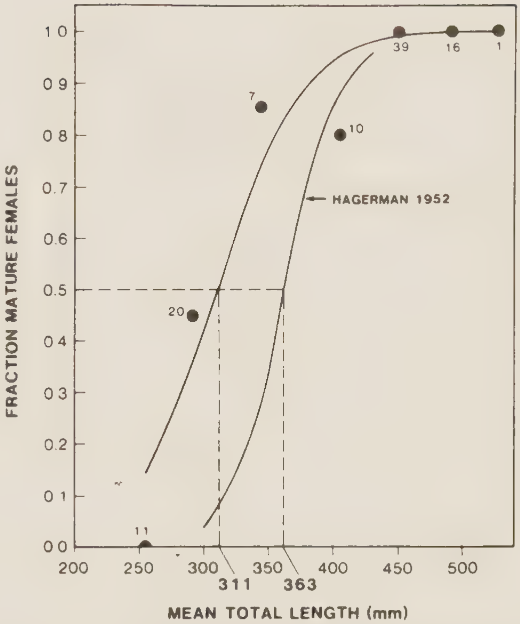

Figure 11. *Circles*, observed fraction of Dover sole that are mature in December within 50-mm length classes with *N* indicated; *solid line*, calculated fraction mature from logistic regression equation (equation 8); *Hagerman line* calculated similarly; *dashed line*, length at 50% maturity.

Oxygen Minimum Zone

Perhaps the most striking features of the environment occupied by Dover sole are the oxygen minimum and dysaerobic zones. In the 1987 survey the oxygen minimum zone ($O_2 < 0.5$ ml/l) occurred between 640 m (350 fath.) and 1010 m (550 fath.), which is similar to the depth range (280–550 fath.) during 1981–82 reported by Mullins et al. (1985) off Point Sur, California. The dysaerobic zone ($O_2 < 1$ ml/l) began at 457 m (250 fath.). Most sexually mature females were observed in the dysaerobic zone. We estimated that 86% of the spawning biomass existed in the oxygen minimum zone (table 4; figure 12) on the basis of the middle depth stratum (250–549 fath.) used in the 1987 and 1988 surveys (Butler et al. 1989). We also estimated that nearly all (93%) of Dover sole living above the dysaerobic zone were juvenile.

The oxygen minimum zone is also characterized by low temperatures (figure 12). The water in the dysaerobic zone ranged from 5.9°C at 530 m (290 fath.) to 3.2°C at 1262 m (690 fath.), and that in the

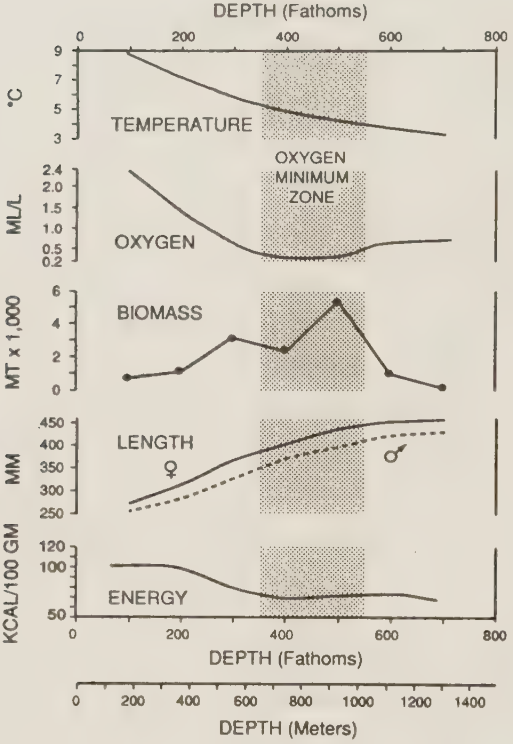

Figure 12. Bottom temperature, dissolved oxygen, biomass (MT) in study area, length (mm), and energy content (kcal/100 g wet weight) of Dover sole as a function of depth for 1987.

oxygen minimum zone from 4.9°C (700 m; 383 fath.) to 4.3°C (902 m; 493 fath.). Reduced metabolism due to temperature may help Dover sole cope with the low oxygen concentrations in the region.

DISCUSSION

Maturity

Our estimate of the length at first maturity differs from that estimated by Hagerman (1952). We fit equation 8 to Hagerman's data (250–630 mm, n = 846) and estimated the length at 50% maturity of female Dover sole landed in Eureka, California, during 1948–49 to be 363 mm ($a = -17.85$, SE of $a = 1.975$, $t = -9.042$, d.f. = 842, $p < 0.01$; $b = 0.0492$, SE of $b = 0.0050$, $t = 9.829$, d.f. = 842, $p < 0.01$; and $n = 844$). We compared the coefficients of the logistic regressions for our data to those collected by Hagerman using the Z-test (Zar 1984;

TABLE 4
Computation of the Proportion of Spawning Biomass of Female Dover Sole (O) in the Oxygen Minimum Zone (OMZ[a])

Variables		1987				1988				1987 + 1988			
Symbol	Definition	Above	In	Below	All zones	Above	In	Below	All zones	Above	In	Below	All zones
B	Total biomass[b] ± 2SE (MT)	2,677 907	13,154 2,899	824 499	16,655 2,161	3,216 1,024	14,054 2,891	26 18	17,297 2,013	2,946	13,604	425	16,975
R	Female wt.[c] Female + male wt.	0.77	0.81	0.92	—	0.77	0.81	0.92	—	0.77	0.81	0.92	—
Q	Female biomass [B x R]	2,061	10,655	758	13,474	2,476	11,384	24	13,884	2,268	11,019	391	13,679
W	Average female weight (g)	275	814	1,122	—	294	840	976	—	278	819	1,118	—
S	Fraction female with active ovaries[d]	0.420	0.736	0.816	—	0.420	0.771	0.816	—	0.420	0.743	0.816	—
O	Spawning female biomass [Q x S] (MT)	866	7,842	618	9,326	1,040	8,777	20	9,836	953	8,187	319	9,459
	(Percent)	9	84	7	100	11	89	<0.1	100	10	86	3	100

[a] Oxygen minimum zone O, < 0.5 ml/l; depth 250–549 fath. Above OMZ, depth < 250 fath.; below OMZ, depth ≥ 550 fath.

[b] From Butler et al. 1989. The biomass numbers for 1987 + 1988 are an arithmetic mean of the separate years' estimates.

[c] Estimated for 1985, 1987, and 1988 trawl survey data combined (no estimate made for individual years; from C. H. Lo, unpublished data, SWFC).

[d] $F = 0.28e^{[illegible]}$, stratum 1; $F = 0.152e^{[illegible]}$, stratum 2; and $F = 0.78e^{[illegible]}$, stratum 3; where $T = -15$ and W = average female weight. The same equations were used for 1987 and 1988 estimates because they were computed by combining survey data from 1985–88 (from C. H. Lo, unpublished data, SWFC).

TABLE 5
Comparison of the Coefficients for Logistic Length and Maturity Equations for Female Dover Sole

	a	Variance	*Z*	*b*	Variance	*Z*
Present study	−9.947	4.661	2.702	0.03202	0.000047	−2.025
Hagerman (1952)	−17.854	3.901		0.04921	0.000025	

table 5). Because both sample sizes were large, we used the normal deviate Z with critical value of $> |2|$. The regression coefficients are significantly different at the .05 level, assuming that these distributions are normal. Thus it appears that Dover sole females from central California matured in 1985 at a smaller size than did those from Eureka, California, in the 1940s. For example, 50% of female Dover sole from central California mature when they reach 311 mm, whereas 50% maturity occurred at 363 mm in females from Eureka (1948–49). This 52-mm difference may be equivalent to an average difference in the age of first maturity of four to five years (assuming fish from central California in the 1980s grew at about the same rate as fish from Eureka in the late 1940s).

Similarly, Yoklavich and Pikitch (1989) compared their 1985 maturity estimate for Dover sole from Oregon to one made for the same area 35 years earlier. They found all females greater than 320 mm were mature in 1985, whereas 35 years earlier (Harry 1959) only 50% of Oregon females of 380 mm were mature and only 15% of the Dover sole less than 380 mm were mature. Yoklavich and Pikitch concluded that Dover sole from Oregon presently mature at smaller size and probably younger age than they did 35 years ago.

Because of possible sampling biases, we hesitate to attribute the differences between recent and older estimates to real biological differences. Bias could result from failure to obtain a representative sample over the full bathymetric range of Dover sole. In addition, the two older estimates (Hagerman 1952 and Harry 1959) may be biased because samples were taken from the fishery during spawning season. This process could lead to an overestimate of the average size of fish at first maturity, because females in postspawning condition could have been wrongly classified as immature. On the other hand, the methods employed by ourselves and Yoklavich and Pikitch (1989) were similar; in both studies the samples were taken in December 1985, which is early enough in the spawning season that biases from misclassification of postspawning fish seem unlikely. If our samples and those of Yoklavich and Pikitch (1989) accurately represent their respective regional populations, then females in Oregon matured at a smaller size than those in central California. For example, all Oregon females longer than 320 mm were mature, whereas in central California, only 57% (SD = 8%) of 320-mm females were mature. Yoklavich and Pikitch (1989) suggest that the long-term effects of the size-selective trawl fishery off Oregon was a compensatory decrease in the size of first maturity of Dover sole. This hypothesis may also explain the difference between our estimates for central California and theirs for Oregon, since the central California fishery (Morro Bay) for Dover sole is a new fishery with only minor landings until the last four or five years, whereas the Dover sole fishery in Oregon has been active for over forty years.

High Water Content

High water content (jellied flesh) has been reported for four marine flatfishes: Dover sole (Fisher et al. 1987; Puckett 1989); winter flounder, *Pseudopleuronectes americanus* (Pearcy 1961); yellowfin sole, *Limanda aspera* (Kizevetter et al. 1965); and American plaice, *Hippoglossoides platessoides* (Templeman and Andrews 1956). Roff (1982, 1983) attributed high water content in flatfishes to degradation of muscle tissue during periods of gonad development and maintenance during winter fasting (Roff 1982, 1983). On the other hand, Puckett (1989) concluded after examining the water content of Dover sole that depth, annual reproductive cycles, size, age, and the onset of sexual maturity were all involved, but depth was the most important factor. Most significantly, Puckett's analysis indicated that reproductive condition of mature females living at 650–1020 m was not correlated with their water content. He found that the average water content of males and females from deep water remained high throughout the year; for example, quarterly means for females ranged from 89.6% in the winter to 91.6% in the spring. He concluded that the effect of the reproductive season on water content was minimal, and that movement into a deepwater habitat was the key variable.

Dover sole differ from other flatfishes with high water content in two ways: the adult population lives at considerable depths (800–1500 m) and in the oxygen minimum zone. In deep-sea fishes, the caloric density per g wet weight typically decreases with depth (Somero et al. 1983). The change in caloric density of Dover sole with depth follows a similar pattern (figure 12). The water content of deep-living Dover sole is at the high end of the range for the deep-sea fishes examined by Childress and Nygaard (1973), where 90.5% was the highest value recorded. This indicates that the ontogenetic change in water content in Dover sole may be simply an adaptation to deepwater existence, and the explanations proposed for low caloric density of deep-sea fishes may apply equally well to Dover sole. These include the scarcity of food and development of feeding strategies that permit a great reduction in propulsive systems demanding a high metabolic rate (Somero et al. 1983).

Another plausible explanation for high water content is one linked to life in the oxygen minimum zone. The oxygen and energy required to maintain white muscle in the oxygen minimum zone could be significant. Reduction of white muscle content would reduce basal oxygen demand and increase the scope for activity in an oxygen-limited environment.

In contrast to white muscle, red muscle tissue is conserved in Dover sole. This red muscle is located behind the head and at the base of the pectoral fin. This location may indicate a role in feeding. Feeding behavior has been described for the congeneric lemon sole, *Microstomus kitt*, by Steven (1930). This species feeds on polychaetes and also inhabits muddy bottoms. When feeding, a lemon sole raises its head and tail and sits perched on its side, scanning the substrate. When a polychaete is found, the fish pounces with a forward leap, bringing its head down on the prey and strongly arching the anterior body (Steven 1930). Dover sole also feed on polychaetes (Pearcy and Hancock 1978; Gabriel and Pearcy 1981; and Wakefield 1984), and we have observed similar feeding behavior in captive Dover sole in our laboratory. Dover sole perched on the substrate have also been observed by Allen (1982) and Wakefield (pers. comm., October 1988). Conserving red muscle while sacrificing white muscle as the fish becomes more watery may be a mechanism to preserve levels of feeding performance while reducing basal oxygen demand.

Ontogenetic and Seasonal Movements

Tagging studies (Westrheim and Morgan 1963; Quirollo and Kalvass 1987) and fishery data (Alverson 1960) indicate that Dover sole move inshore in the summer. This raises some interesting questions concerning the ontogenetic movements we have described. Do the fish precisely re-sort themselves by depth each fall as they leave their shallow summer habitat? How do they gradually (over decades) increase the depth of their winter habitat? Does high water content affect the extent of seasonal movements?

No data exist to fully answer these interesting questions, but some inferences can be made on the basis of a tagging study conducted by Quirollo and Kalvass (1987). Their data indicate that all Dover sole may not participate in the summer inshore movement. Mature fish tagged and released in shallow water were usually recovered from deep water in the winter and fall and from shallow water in the spring and summer, indicating annual inshore movement. In contrast, most of the mature fish tagged and released in deep water were recovered in deep water regardless of season. Thus the tagging data indicate that two substocks may exist, one that migrates and one that does not. We suggest that the fish composing the migratory substock may be younger and have a lower water content than those composing the nonmigratory substock.

CONCLUSIONS

The deep, cold, and poorly oxygenated region of the continental slope known as the oxygen minimum zone is the habitat for the mature Dover sole in central California. Ninety-eight percent of the spawning biomass of Dover sole occurs in this region. Dover sole spawn at these depths, and their eggs rise to the surface layers.

Juveniles settle on the continental shelf and, with sexual maturity, gradually move down the continental slope. The onset of sexual maturity and the ontogenetic movement into the cold oxygen minimum zone (350–550 fath.; 640–1010 m) is usually associated with an increase in water content, myoglobin content of red muscle, and fat stores. The movement down the slope corresponds with a consistent pattern of increasing size, age, and water content.

The ontogenetic movement down the shelf is gradual and occurs over decades. The average female Dover sole in central California reaches maturity when about 7 years old and 311 mm long. At this time she lives at a depth of about 329 m (180 fath.), and her water content is about 83.8%. We speculate that over the next nine years the annual inshore and offshore movement gradually ceases. Over the same period the water content of the average female gradually increases as she descends to greater depths and enters the oxygen minimum zone (640 m; 350 fath.). By then she is 16 years old, is almost 400 mm long, and has a water content of 87%. By this time she, like 93% of her cohort, is sexually mature, and growth has slowed from 14 mm per year when she was 7 years old to 6 mm per year. Eleven years later the average female has descended to 1006 m (550 fath.), is 27 years old, has grown 44 mm (about 4 mm per year), and has a water content of 88.7%. Water content continues to increase slowly over the next decades, and the fish continue to spawn and move deeper. The oldest female we aged was 51 years. The highest water content was 94.1%. The greatest depth at which we collected Dover sole was 1269 m.

LITERATURE CITED

Allen, M. J. 1982. Functional structure of soft-bottom communities of the Southern California Shelf. Ph.D. thesis, Univ. Cal. San Diego, 577 pp.

Alverson, D. L. 1960. A study of annual and seasonal bathymetric catch patterns for commercially important groundfishes of the Pacific Northwest coast of North America. Pac. Mar. Fish. Comm. Bull. 4, 66 pp.

Butler, J. L., C. Kimbrell, W. C. Flerx, and R. D. Methot. 1989. The 1987–88 demersal fish surveys off central California (34°30′N to 36°30′N). Southwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo. TM-NMFS-SWFC-133, 44 pp.

Childress, J. J., and M. H. Nygaard. 1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. Deep-Sea Res. 20:1093–1109.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 pp.

Demory, R. L. 1972. Scales as a means of aging Dover sole (*Microstomus pacificus*). J. Fish. Res. Board. Can. 29:1647–1650.

Dobush, G. R., C. D. Ankney, and D. G. Krementz. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. Can. J. Zool. 63:1917–1920.

Draper, N., and H. Smith. 1981. Applied regression analysis. New York: John Wiley & Sons, 709 pp.

Engelman, L. 1988. LR stepwise logistic regression, *In* BMDP statistical software manual, vol. 2, W. J. Dixon, ed. Pp. 941–969.

Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific Coast fishes of North America. Boston: Houghton-Mifflin Co., 336 pp.

Fisher, R. A., R. A. Fritzche, and G. L. Hendrickson. 1987. Histology and ultrastructure of the 'jellied' condition in Dover sole, *Microstomus pacificus*. Proc. V Congr. Europ. Ichthyol., Stockholm 1985, pp. 345–350.

Gabriel, W. L., and W. G. Pearcy. 1981. Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon. Fish. Bull., U.S. 79(4): 749–763.

Hagerman, F. B. 1952. The biology of the Dover sole (*Microstomus pacificus*) (Lockington). Calif. Dep. Fish Game Fish Bull. 85, 48 pp.

Harry, G. Y. 1959. Time of spawning, length at maturity, and fecundity of the English, petrale and Dover soles (*Parophrys vetulus*, *Eopsetta jordani* and *Microstomus pacificus*, respectively). Fish. Comm. Oregon. Res. Briefs 7(1):5–13.

Hendrickson, G. L., R. A. Fritzsche, and H. M. Puckett. 1986. Ecology and possible causes of the "jellied" condition in Dover sole, *Microstomus pacificus*. California Sea Grant biennial report, 1982–1984, University of California Sea Grant College Program, Rep. No. R-CSGCP-020:129–130

Kizevetter, I. E., E. F. Kleie, A. A. Kirillova, O. M. Mel'Nikova, V. M Myasoedova, and L. Ya. Ertel. 1965. Technological characteristics of Bering Sea fishes, *in* Soviet fisheries investigations in the northeast Pacific. Part VI, P. A. Moiseev, ed. (Transl. from Russian by Israel Program for Sci. Trans., Jerusalem, 1968.) Pp. 191–258.

Mearns, A. J., and L. Harris. 1975. Age, length, and weight relationships in southern California populations of Dover sole. S. Cal. Coast. Water Res. Proj. TM 219, 17 pp.

Mullins, H. T., K. McDougall, and T. L. Vercoutere. 1985. Oxygen-minimum zone edge effects: evidence from the central California coastal upwelling system. Geology 13:491–494.

O'Neill, R. 1971. Function minimization using a simplex procedure. Algorithm AS47. Applied Statistics, 338.

Paine, R. T. 1971. The measurement and application of the calorie to ecological problems. Annu. Rev. Ecol. Syst. 2:145–164.

Parr Instrument Co. 1960. Oxygen bomb calorimetry and combustion methods. Technical Manual No. 130, 1–56. Moline, Ill.

Pearcy, W. G. 1961. Seasonal changes in osmotic pressure of flounder sera. Science 134:193–194.

Pearcy, W. G., and D. Hancock 1978. Feeding habits of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*, slender sole, *Lyopsetta exilis*; and Pacific sanddab, *Citharichthys sordidus*, in a region of diverse sediments and bathymetry off Oregon. Fish. Bull., U.S. 76:641–651.

Pearcy, W. G., M. J. Hosie, and S. L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. Fish. Bull., U.S. 75:173–183.

Pikitch, E., and R. Demory. 1988. Assessment of scales as a means of aging Dover sole. Trans. Am. Fish. Soc. 117:345–349.

Puckett, H. M. 1989. Ecology and possible causes of the jellied condition in Dover sole (*Microstomus pacificus*). M.S. thesis, Humboldt State Univ., Arcata, Calif., 80 pp.

Quirollo, L. F., and P. Kalvass. 1987. Results of Dover sole tagging in waters off northern California, 1969–1971. Calif. Dep. Fish Game Mar. Res. Admin. Rep. No. 87–4, 73 pp.

Roff, D. A. 1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686–1698.

———. 1983. An allocation model of growth and reproduction in fish. Can. J. Fish. Aquat. Sci. 40:1395–1404.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman and Co., 859 pp.

Somero, G. N., J. F. Siebenaller, and P. W. Hochachka. 1983. Physiological adaptations of deep-sea animals. *In* The sea, vol. 8: deep-sea biology, G. T. Rowe, ed. N.Y.: Wiley Interscience.

Steven, G. A. 1930. Bottom fauna and the food of fishes. J. Mar. Biol. U.K. 16:677–706.

Templeman, W., and G. L. Andrews. 1956. Jellied condition in the American plaice *Hippoglossoides platessoides* (Fabricius). J. Fish. Res. Bd. Can. 13:147–182.

Wakefield, W. W. 1984. Feeding relationships within assemblages of nearshore and mid-continental shelf benthic fishes off Oregon. M.S. thesis, Oregon State Univ., Corvallis, Oregon, 102 pp.

Westrheim, S. J., and A. R. Morgan. 1963. Results from tagging a spawning stock of Dover sole, *Microstomus pacificus*. Pac. Mar. Fish. Comm. Bull. 6:14–21.

Yoklavich, M. M., and E. K. Pikitch. 1989. Fecundity and status of maturity of Dover sole, *Microstomus pacificus*, off northern Oregon, Fish Bull., U.S. 87(4).

Zar, J. H. 1984. Biostatistical analysis. New Jersey: Prentice-Hall, 718 pp.

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Determination of Factors Affecting Recruitment of Chinook Salmon *Oncorhynchus tshawytscha* in Central California

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Abstract.–We computed correlations between various population estimates for Central California chinook salmon *Oncorhynchus tshawytscha* and both freshwater and marine environmental variables using methods that account for intraseries correlation in a more accurate and conservative way than those used previously. These indicated a negative influence of ENSO (El Niño-Southern Oscillation) conditions in the year during which most of these fish are caught or leave the ocean to spawn. Although freshwater environmental influences have been previously proposed on the basis of correlation analysis, and have been demonstrated using direct survival estimates based on marked fish, they were not detectable using correlation techniques that accurately account for intraseries correlation. There was also weak evidence for an influence of conditions associated with a negative upwelling index at the time chinook salmon enter the ocean. However, because these conditions are associated with high river flows in addition to oceanographic effects, these correlations may merely result from the influence of freshwater flows. To further describe oceanographic influences we computed the principal components of upwelling index, sea level height, and sea surface temperature. The first principle component, which reflected the effects of ENSO conditions in the equatorial Pacific during the previous winter, was significantly correlated with chinook salmon abundance in their final year, and marginally correlated with abundance during the first ocean summer. This work demonstrates new techniques for reducing spurious correlations and the practical difficulties involved in sorting out the multivariate influences on populations subject to remote forcing through oceanographic and meteorological conditions.

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Understanding the influences of environment on survival and abundance of chinook salmon *Oncorhynchus tshawytscha* is necessary for management of both fisheries and surface water in central California. The salmon fisheries are managed by allocating predicted preseason abundance between catch and spawning escapement, and flow rates in central California rivers are currently managed to allow adequate flows for spawning and rearing of chinook salmon. Better understanding of environmental influences on salmon populations could improve the ability to forecast preseason abundance and more clearly define the impacts of water management on salmon abundance.

Chinook salmon spawn in freshwater, but spend most of their lives in the ocean. In California's Central Valley, there are four distinct runs of chinook salmon named for the timing of their spawning migrations: fall, late-fall, winter, and spring. Typically over 90% of the spawning salmon are from the fall run, and over 80% spawn in the Sacramento River and its tributaries (USFWS 1987). Fall run chinook salmon migrate upstream July through November, and spawn October through January. Eggs incubate in the gravel October through March, and young fish rear in the streams and migrate downstream December through June (USFWS 1987). Most fish spawn at age 3, with some spawning at ages 2 and 4, and a few fish at age 5 (Dettman et al. 1986, Reisenbichler 1986, Kope 1987). The precocious 2-year-old spawners are primarily males and are called "jacks." While in the ocean, Central Valley chinook salmon are harvested by commercial and recreational troll fisheries. Catches in both fisheries are dominated by 3-year-old fish (Denega 1973, Kope 1987).

In addition to natural production, several hatcheries and spawning facilities produce fish to enhance the fisheries and mitigate for losses of spawning and rearing habitat resulting from water development projects (Fig. 1). The contribution of hatchery production to spawning runs has increased in recent years, and has been estimated to be approximately 15% of the total run in the upper Sacramento River (Reisenbichler 1986), 78% of the run in the Feather River, and 87% of the total in the American River (Dettman and Kelley 1986).

Numerous studies have examined relationships between environmental

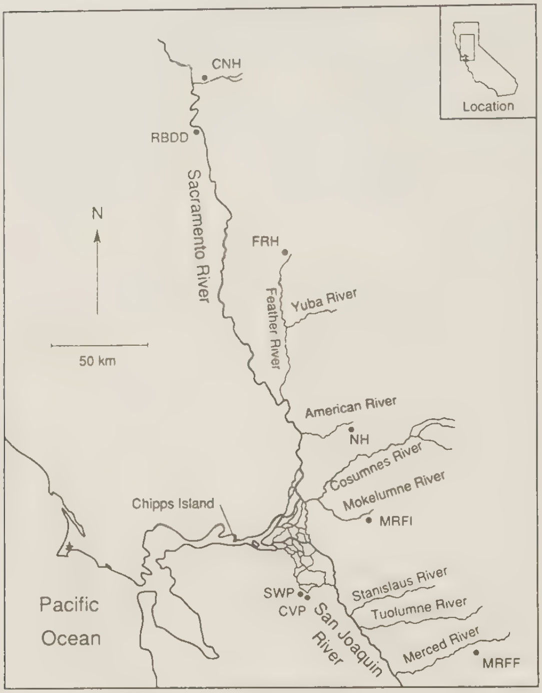

Figure 1

Chinook salmon spawning streams and fish facilities of California's Central Valley. CNH = Coleman National Hatchery; RBDD = Red Bluff Diversion Dam; FRH = Feather River Hatchery; NH = Nimbus Hatchery; MRFI = Mokelumne River Fish Installation; MRFF = Merced River Fish Facility; SWP = State Water Project pumping plant; CVP = Central Valley Project pumping plant.

variables and recruitment or abundance of Pacific salmonids through correlation analysis. Many of these studies have focused on chinook salmon (e.g., Van Hyning 1973, Barton 1980), and a few have dealt with the stock of chinook salmon that spawns in California's Central Valley. Most of these studies have detected environmental influences on recruitment; but in the case of Central Valley chinook salmon, reasonably long time-series of recruitment data have been lacking. Some analysts have therefore used estimates of spawning escapement as a proxy for past recruitment (Dettman et al. 1986, Dettman and Kelley 1986, Reisenbichler 1986, USFWS 1987). In general, these studies have reported positive correlations with flow variables and negative correlations with temperature during the period when the spawners were migrating downstream as smolts. Because of a negative correlation between flow variables and temperatures (Dettman et al. 1986), it is impossible to distinguish between effects of temperature and effects of flow using existing data. Stevens and Miller (1983) used two time-series of smolt estimates based on smolt catches in the delta (Fig. 1), and showed a positive correlation with flows in the previous winter. The most convincing studies used estimates of mortality based on the difference in survival between tagged fish released above the delta and tagged fish released below the delta to show a positive influence of flow rates in the delta and negative influences of temperature and diversions (Kjelson and Brandes 1989, Kjelson et al. 1981, USFWS 1987, Dettman et al. 1986).

In contrast to those of freshwater, potential marine influences on Central Valley chinook stocks have not been explored. Oceanographic conditions off the California coast vary dramatically providing potentially important interannual differences in predators, prey, transport, and ocean temperature during the marine phase of chinook salmon life. The normal pattern of circulation in the northeastern Pacific involves northwesterly winds of varying strength along the coast of California in the spring and summer months which reinforce the geostrophic flow of the California Current and transport surface waters offshore (Mysak 1986, Hickey 1989). This causes varying degrees of upwelling of deeper water and longshore advection of subarctic water along the coast of California and Oregon, which are associated with colder temperatures and depressed sea level heights. The amount of upwelling is estimated by an upwelling index based on winds computed from measured atmospheric pressure gradients (Bakun 1975). Occasional El Niño-Southern Oscillation (ENSO) events, characterized by a warming of equatorial Pacific waters, have a dramatic effect on California coastal waters. These effects may result from either coastal trapped waves which propagate poleward from the Equator, or an atmospheric teleconnection between the Equator and midlatitudes (Emery and Hamilton 1985, Mysak 1986). The former would cause higher sea surface temperatures and sea level heights, but would not necessarily affect Bakun's upwelling index (Enfield and Allen 1980, Emery and Hamilton 1985, Mysak 1986). The latter involves an increase in strength of the Aleutian low-pressure system and a weakening of the north Pacific high-pressure system. Changes in the atmospheric pressure gradients, associated with ENSO events, weaken the northerly winds which results in less upwelling, warmer sea temperatures, higher sea level, and a lower upwelling index (Norton 1987, Mysak 1986). ENSO events and anomalous strengthening of the Aleutian low pressure system may occur at the same time, but each also occurs alone (Emery and Hamilton 1985, Mysak 1986).

Marine and freshwater influences on California Central Valley chinook salmon could be confounded. Large-scale oceanographic and meteorological conditions in the Pacific have been related to precipitation in California, which could in turn influence flow rates. Markham and McLain (1977) found a positive correlation between California rainfall and sea surface temperature off the coast of Washington. However, rainfall in California is only weakly related statistically to equatorial conditions associated with ENSO events (Douglas and Englehart 1981, Cayan and Peterson 1989, Redmond 1988).

Environmental influences on fish populations are often explored by computing correlations between environmental and population time-series; however, these are computed and the significance of resulting correlations are evaluated in a variety of ways. In attempting to detect environmental influences by computing correlations, the probability of obtaining a significant result is often artificially inflated by two problems: (1) intraseries correlation and (2) multiple tests (cf. Walters and Collie 1988). The latter arises from the fact that many environmental series can be tested for correlation with the population series; hence the probability of falsely identifying a significant relationship is greater than the probability level of each test. Methods exist for dealing with both problems, but we focus on the former here [see Hollowed et al. (1987) and Drinkwater and Myers (1987), for examples of dealing with the latter]. The former, intraseries correlation, is a lack of statistical independence of observations, which implies that the true number of degrees of freedom that should be used in determining the significance of a computed correlation is less than the number of points in the series. There are two steps that can be taken to deal with this problem: (1) removing as much of the intraseries correlation as possible, and (2) accounting for the remaining correlation in the computation of confidence limits.

Removal of intraseries correlation can be accomplished by arbitrarily "pre-whitening" the series (i.e., filtering the series so that correlation between adjacent points is removed) (Box and Jenkins 1976, Fogarty 1988), but is more directly justified when there is a physical basis for doing so and the new series represents a meaningful quantity. In the case of an abundance or catch series, one can compute a recruitment time-series from the original series using deconvolution (Kope and Botsford 1988). Deconvolution is a procedure based on the observation that catch or abundance is a sum over age-classes which is essentially a weighted sum over past recruitment (i.e., a moving average), in which the weighting factors are the (assumed constant) probabilities of survival to each age. If the abundance or catch series is established using a size limit, rather than an age limit, the numbers at each age that are larger than the size limit must also be accounted for in the weighting factors. Deconvolution inverts this summing process to give recruitment in terms of catches or abundances. Deconvolution provides two advantages over using the catch or abundance series without deconvolution: (1) it removes the intraseries correlation due to summing ages in abundance or catch data, and hence provides more conservative estimates of the significance of correlations between recruitment and the environment; and (2) it yields an estimate of recruitment from the abundance or catch data, hence it can also increase the magnitude of estimated correlation coefficients. However, deconvolution cannot yield an exact value of recruitment when noise is present in the abundance or catch data. The error present in the recruitment estimates depends on the error present in the catch or abundance series and on the stability of the deconvolution (Kope and Botsford 1988). Thus, there is a trade-off between the two advantages of removing the effects of multiple age-classes and the disadvantage of amplifying errors that depends on the stability of the deconvolution and the magnitude of measurement errors in abundance. Consequently, deconvolution may not always be useful.

Intraseries correlation is accounted for in the computation of confidence limits by estimating the variance of the computed correlation coefficient in a way that accounts for the intraseries correlation. This often involves using one of the many approximations to an expression originally due to Bartlett (1946) (Box and Jenkins 1976, Chelton 1984, Botsford 1986). This approach is functionally equivalent to adjusting the number of degrees of freedom using a variation of the expression originally due to Bayley and Hammersley (1946) (Sutcliffe et al. 1976, Drinkwater and Myers 1987). We use another method for dealing with this problem that leads to an actual probability of detection that is closer to the specified probability than other methods (Kope and Botsford 1988, Botsford and Wainwright unpubl.).

In spite of the fact that greater intraseries correlation artificially inflates the probability of detecting a significant relationship, some researchers have added intraseries correlation to the time-series before computing correlations. For example, in the freshwater chinook salmon studies cited above, Dettman et al. (1986) and Reisenbichler (1986) used 2-year moving averages of both spawning escapement and environmental variables in an effort to reduce the effects of age structure in the spawning escapement data. Hollowed et al. (1987) used five-point moving averages in their analysis of recruitment patterns in the northeast Pacific. Because the effects of intraseries correlation were not accounted for in either of these studies, the use of moving averages would decrease the probability of detecting real correlations and increase the probability of spurious correlation (Kope and Botsford 1988). Others have used moving averages before computing correlations, but then have attempted to account for increased intraseries correlation [cf. Drinkwater and Myers (1987), who use a modified form of the Bayley and Hammersley (1946) approach].

The goals of the study reported here are to explore potential environmental influences on chinook salmon populations in California's Central Valley, and to demonstrate the effective use of some recently developed methods of correlation analysis that are more realistic and conservative than those used previously. We identify potential oceanographic environmental influences on these populations and show that the freshwater influences, which were established by direct survival estimates (USFWS 1987, Kjelson and Brandes 1989), are not detectable from correlation analysis of the available environmental and population data.

Data and methods

Environmental data were obtained from four sources. Average monthly streamflow data were obtained from published USGS records for gauging stations at Verona on the upper Sacramento River, Nicholas on the Feather River, and Fair Oaks on the American River. Flow and diversion data for the Sacramento-San Joaquin delta were obtained from the California Department of Water Resources DAYFLOW hydrological model. Data on sea surface temperature at the Farallon Islands, southern oscillation index, and tidal height at San Francisco (37.48 N 122.22 W) were obtained from D. Cayan (Scripps Inst. Oceanography, La Jolla, CA 92037), and calculated coastal upwelling index at lat. 39°N (Bakun 1975) was obtained from A. Bakun (Pacific Fish. Environ. Group, Natl. Mar. Fish. Serv., NOAA, Monterey, CA 93940).

Population data were taken from the recreational fishery, the commercial fishery, and spawner estimates. We used spawner data from the upper Sacramento River, the Feather River, the Yuba River, and the American River. In the available data, adults had been separated from jacks on the basis of length. Fish less than 60.7 cm fork length were taken to be jacks and larger fish were counted as adults. For the period 1970–86, spawning stock estimates were obtained from Pacific Fishery Management Council (PFMC) reports. For the years 1962–69, total fall-run spawners were taken from Fry and Petrovich (1970), and adult spawners were estimated by multiplying the total estimate of fall-run spawners in each stream by the fraction of carcasses classified as adults in the spawning stock surveys. In addition to abundance indices from individual streams, total adult spawners for the entire Central Valley were estimated by multiplying the fraction of adults reported in all spawning stock surveys each year by the number of spawners in all runs for all rivers combined.

Commercial and sport catch south of Point Arena were obtained from PFMC reports for the years 1971–86, and from L.B. Boydstun (Calif. Dep. Fish Game, Region II, Rancho Cordova, CA 95670, unpubl. data) for the years 1962–70. Commercial effort, measured in thousands of landings, and sport effort, measured in thousands of angler days, were obtained or calculated from the same sources. Fishing effort was used to calculate catch-per-unit-effort (CPUE) in an attempt to remove some of the effects of variable fishing effort from the catch data.

Recruitment of year-classes at the beginning of the commercial fishing season in their second year of life was estimated by deconvolution of the abundance indices using the procedure described in Kope and Botsford (1988). This involved calculating the contribution of recruitment in each year to the abundance indices in subsequent years using an age-structured catch and escapement model with population parameters estimated by separable virtual population analysis of marked hatchery fish (Kope 1987). In addition to the recruitment estimates obtained by deconvolution of the individual abundance series, we estimated recruitment by deconvolving the combined abundance series. This combined deconvolution was obtained by adding together commercial catch, sport catch, and total spawning escapement for each year, and deconvolving the combined abundance series (Kope and Botsford 1988).

Examination of the different recruitment estimates revealed that the deconvolved spawner series contained a great deal of high-frequency noise which resulted from the marginal stability of the deconvolutions of spawner indices. Because of differences in the relative contribution of each age-class, the deconvolution of total spawners was inherently much less stable than the deconvolution of adult spawners (Kope and Botsford 1988). Because recruitment estimates from spawners (adults and jacks) and adult spawners were highly correlated with one another (hence probably represent the same signal, and the deconvolved adult spawners contain less introduced error), only deconvolved adult spawners were used as recruitment estimates derived from spawning escapement.

No attempt was made to separate natural production from hatchery fish in the spawning escapement. Because of the large contribution of hatchery fish to the spawning runs (cf., Reisenbichler 1986, Dettman and Kelley 1986) and the straying of hatchery fish (Hallock and Reisenbichler 1979, Sholes and Hallock 1979), accurate estimation of the natural component of the runs was not possible.

Before computing correlations with environmental data, we tested for an influence of density on the pop-

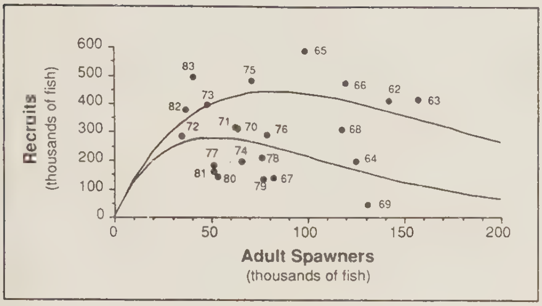

Figure 2

Chinook salmon stock-recruitment curves for the main stem of the Sacramento River. Upper curve was fitted to the data for brood years 1962–66 and the lower curve was fitted to 1967–83.

ulation series. Stock-recruitment relationships for the Sacramento, Feather, and American Rivers were examined by plotting recruitment against spawning stock, and fitting Ricker stock-recruitment curves to the data by the standard linear-regression method. This approach can result in substantial biases in the estimates of stock-recruitment parameters that result from the correlation between recruitment and subsequent spawning stock (Walters 1985, Kope 1988). However, because we use stock-recruitment curves only as a visual aid in interpreting the stock-recruitment data, potential bias was not evaluated.

To examine possible relationships between recruitment and the environment, correlations were computed between time-series of recruitment and quarterly averages of the environmental variables at all lags that had potential biological meaning. These quarterly averages are referred to as: winter, January–March; spring, April–June; summer, July–September; fall, October–December. Correlations with individual stream flows were computed at lags that corresponded to the winter, and to spring while the fish were resident in the streams as fry or migrating downstream. Correlations with delta flows and diversions were computed for the spring while the fish were migrating to sea, and correlations with oceanographic variables were computed from the spring in the year that fish migrated to sea through the summer 2 years later when most fish mature and leave the ocean to spawn. Correlations involving abundance indices (i.e., catch and spawning escapement series) were computed at lags that assumed the indices consisted primarily of 3-year-old fish.

Variability on all time scales can contribute to the variance of time-series and to the magnitude of calculated correlation coefficients. However, variability on greater than annual time scales involves intraseries correlation, which implies the effective number of degrees of freedom is less than the number of years in the series. Linear trends in the time-series reflect variability on time scales that: (a) can easily be removed by detrending, and (b) are not detectable with existing data. We have removed linear trends from our time-series because they may obscure a relationship on faster time scales.

Intraseries correlation due to variability on intermediate time scales was accounted for in evaluating the significance of computed correlation coefficients. The variance of computed crosscorrelation coefficients can be approximated by

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \sum_{i=1-n}^{n-1} \left(1 - \frac{|i|}{n}\right) \rho_{xx}(i)\, \rho_{yy}(i) \qquad (1)$$

where n is the number of data pairs, $\rho_{xx}(i)$ and $\rho_{yy}(i)$ are the autocorrelation functions of the two time-series variables at lag i, and $r_{xy}(t)$ is the computed crosscorrelation coefficient between the two time-series at lag t (Botsford and Wainwright unpubl., Kope and Botsford 1988). When no intraseries correlation is present, this expression simplifies to

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \qquad (2)$$

Because the real values of the autocorrelation functions of time-series variables are unknown, and computed autocorrelation coefficients must be used instead, expression (1) can sometimes produce variance estimates smaller than expression (2). However, expression (2) places a lower bound on the possible variance of computed crosscorrelation coefficients because it approximates the variance in the best possible case, when no intraseries correlation is present. We estimated the significance of computed crosscorrelation coefficients by assuming a normal distribution with variance given by the greater of expressions (1) and (2). This strategy has performed the best in giving appropriate rejection rates in Monte Carlo simulations for independent random series with varying degrees of intraseries correlation (Botsford and Wainwright, unpubl. data).

Results

Exploration of possible density-dependence revealed no clear relationships that could be removed prior to examining the influence of environmental variables. The stock-recruitment relationship for the upper Sacramento River appears to show a decrease in the equilibrium stock size that coincides with the closure of Red Bluff Diversion Dam in 1966 (Fig. 2). This supports the

Table 1

Correlations of chinook salmon population estimates with freshwater flow variables in the Sacramento Valley, California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Feather River adult spawners	Delta diversions	1st spring	0.456**
Feather River recruits (deconvolved adult spawners)	Delta diversions	1st spring	0.424**
Total adult spawners	Delta inflow	1st spring	0.402*
	Delta outflow	1st spring	0.393*

*$p<0.10$, **$p<0.05$

Table 2

Correlations with combined California Central Valley fall-run chinook salmon spawning stock indices. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Total adults	UPW	1st spring	−0.542***
		1st summer	−0.444*
	SST	3rd spring	−0.427**
		3rd summer	−0.593***
Recruits (deconvolved adults)	SLH	3rd summer	−0.425**
	SST	3rd summer	−0.541***

*$p<0.10$, **$p<0.05$, ***$p<0.01$

argument that the decrease in recruitment is a direct consequence of the dam rather than the result of gradual habitat degradation or increasing fishing pressure (Hallock et al. 1982, Hallock 1983). A similar effect had been observed by Reisenbichler (1986) but he found that the spawning runs resulting from the 1964, 1965, and 1966 brood years were intermediate between the stock-recruit curves associated with the time periods before and after these years. With our deconvolved recruitment estimates, the 1964 brood year appears to have been abnormally low, but 1965 and 1966 appear comparable with earlier years. Data for the Feather River and the American River do not fit stock-recruitment curves as well as the Sacramento River data. Our data include few years before the damming of the Feather River and none for the American River before the construction of Nimbus Dam. On both of these rivers, the hatchery contribution to the spawning escapement is large, hence lack of a clear stock-recruitment relationship is not surprising.

To assess the influence of the freshwater environment on Sacramento Valley stocks, we computed correlations between population variables and environmental variables on three rivers—the Sacramento, the Feather, and the American—as well as the total of these three, and relevant environmental variables. Population variables were total spawners, adult spawners, jacks, and recruitment estimated by deconvolution of adult spawners. We thus tested for environmental effects on all spawners, as well as differential effects on jacks and adults, and recruitment to the adult spawner population. Environmental variables were the flow of each river, total diversions of flow in the Sacramento-San Joaquin Delta, diversions as a percentage of flow, delta inflow, and delta outflow. We present all correlations that were significant at the 0.1 level using the standard uncorrelated series test, and annotate with asterisks the significance of each of these according to the more conservative test that allows for intraseries correlation.

The results (Table 1) provide no evidence for an influence of the freshwater environment on numbers of total spawners, jacks, adults, or adult recruits to these stocks. In fact, the number of correlations significant

Table 3

Correlations between chinook salmon recruitment estimates from ocean abundance indices and environmental variables in Central California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Commercial catch	UPW	1st fall	0.397*
	SLH	1st fall	−0.415**
	SST	2nd spring	−0.437*
		3rd summer	−0.503**
Recreational catch	SST	1st spring	0.711*
		1st summer	0.484**
		2nd winter	0.578
Commercial CPUE	UPW	1st spring	−0.607
		1st summer	−0.448
Recreational CPUE	SST	1st spring	0.583
		2nd winter	0.500
	UPW	1st spring	−0.453
		2nd winter	−0.357
Recruits (deconvolved commercial catch)	UPW	1st spring	−0.460**
	SST	3rd spring	−0.335
Recruits (deconvolved recreational catch)	SST	1st spring	0.353*
Recruits (combined deconvolution)	UPW	1st spring	−0.476**
	SST	3rd summer	−0.538**

*$p<0.10$, **$p<0.05$

at the 0.1 level is half the number expected if all series were independent (i.e., 4 versus 8 out of 80), and the only correlations significant at the 0.05 level using the conservative test—a positive effect of diversions on Feather River fish—has no apparent physical or biological explanation, because diversions during downstream migration would be expected to have a negative effect on survival. We consider this one a spurious correlation. Lack of correlation with delta diversions and total delta outflow may be due in part to the fact that hatcheries on the Feather and American Rivers have released most of their smolts below the delta since the mid-1970s.

Marine influences on spawners were assessed by computing correlations between the same population variables and upwelling index, sea level height, and sea surface temperature. The resulting correlations (Table 2) are significant at the 0.05 level only for adult spawners and recruitment to the adult spawner population. They show a negative influence of conditions associated with ENSO events (i.e., higher ocean temperatures, higher sea levels) in the third spring and summer, immediately before the adults enter the rivers to spawn. There is also a positive correlation with upwelling index in the first spring and summer, during which smolts migrate downriver, through the delta, and enter the ocean.

We also tested for marine and freshwater influences on catch data from both the commercial and the recreational fishery. We attempted to remove the effects of fluctuations in effort from the catch by computing commercial catch-per-unit-effort and recreational catch-per-unit-effort using the marginal effort data. We computed recruitment estimates from deconvolution of each of these. There is a substantial number of correlations significant at the 0.1 level using the standard test, but none reflect freshwater influences (Table 3). Of the correlations that are significant at the 0.05 level, two are with temperature in the third summer, and the remaining four are in the first marine year, three of them being with upwelling index and the other with sea level height. None of the catch-per-unit-effort variables were significantly correlated with any of the environmental variables using the conservative test.

These results indicate that oceanographic conditions during the first and third years of life may influence

Table 4

Autocorrelations of the Southern Oscillation Index (SOI) and crosscorrelations between SOI and oceanographic variables off Central California. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature, PC = principal component. Underlined correlations correspond to an influence of previous SOI on winter oceanographic conditions off California.

	SOI	UPW	SLH	SST	1st PC
Winter SOI					
−9 mo	0.552***	0.478***	−0.205	0.000	−0.253
−6 mo	0.730***	0.261	−0.211	−0.093	−0.279
−3 mo	0.811***	0.208	−0.439**	−0.405**	−0.390*
0	1.000***	0.667***	−0.651***	−0.573***	−0.712***
3 mo	0.256	0.380*	−0.342*	−0.305	−0.449**
6 mo	0.031	−0.140	−0.270	−0.108	−0.168
9 mo	−0.110	0.231	−0.239	−0.133	10.163
12 mo	−0.131	−0.034	−0.042	−0.103	−0.078
Spring SOI					
−9 mo	0.112	0.340*	−0.102	−0.088	−0.202
−6 mo	0.115	0.113	−0.117	−0.330	−0.321
−3 mo	0.256	−0.050	−0.169	−0.165	−0.030
0	1.000***	0.393*	−0.268	−0.298	−0.414*
3 mo	0.825***	0.022	−0.297	−0.328	−0.326
6 mo	0.688***	0.246	−0.540***	−0.402**	−0.406*
9 mo	0.562***	0.424**	−0.389	−0.518***	−0.531***
12 mo	−0.224	−0.094	−0.067	−0.212	−0.129
Summer SOI					
−9 mo	−0.154	0.143	0.190	0.029	−0.070
−6 mo	0.031	−0.091	−0.037	0.007	0.092
−3 mo	0.825***	0.390*	−0.242	−0.191	−0.353
0	1.000***	0.269	−0.337*	−0.350*	−0.448**
3 mo	0.785***	0.200	−0.573***	−0.572***	−0.507***
6 mo	0.761***	0.428**	−0.433**	−0.535***	−0.544***
9 mo	0.109	0.197	−0.147	−0.337	−0.301
12 mo	−0.214	−0.256	−0.021	0.047	0.090
Fall SOI					
−9 mo	−0.110	−0.175	0.063	0.128	0.197
−6 mo	0.688***	0.426**	−0.324	−0.246	−0.406*
−3 mo	0.785***	0.305	−0.211	−0.192	−0.309
0	1.000***	0.164	−0.441**	−0.344*	−0.346
3 mo	0.835***	0.504***	−0.630***	−0.479***	−0.604***
6 mo	0.114	0.233	−0.341*	−0.314	−0.385*
9 mo	−0.152	−0.269	−0.123	0.043	0.010
12 mo	−0.072	0.263	−0.044	0.087	−0.031

*$p<0.10$; **$p<0.05$; ***$p<0.01$

these stocks of chinook salmon. However, because the correlations are with three oceanographic variables rather than consistently with one, they are somewhat difficult to interpret in terms of a causal mechanism. To attempt to solve this problem, we sought a single indicator of variability in the coastal ocean. We computed the principal components (Harris 1975) of variability in sea surface temperature, sea level height, and upwelling index, in the hope that they would have a meaningful physical interpretation. The resulting first principal component is larger than the second and third by about a factor of two, depending on season, and its loading is approximately equal for all three variables (positive for sea level height and ocean temperature and negative for upwelling index). Positive values of sea level height and surface temperature are consistent with the higher latitude effects of ENSO events as would be propagated by coastal trapped waves, but the negative value of upwelling index would require atmospheric teleconnection (recall the upwelling index is not a measure of actual upwelling, but an estimate based on atmospheric pressure

Table 5

Correlations between first principle component of the oceanographic variables and estimated total age-3 abundance (recreational catch + commercial catch + adult spawners) of chinook salmon in Central California.

	Season	First year	Second year	Third year
Total abundance	Winter	0.289	0.101	−0.151
	Spring	0.356*	−0.317	−0.354
	Summer	0.274	−0.139	−0.482**
	Fall	−0.115	0.114	0.080
Deconvolved total abundance	Winter	0.121	0.239	−0.139
	Spring	0.361*	−0.202	−0.319
	Summer	0.166	0.017	−0.480**
	Fall	−0.177	0.108	0.097

*$p<0.10$; **$p<0.05$

differences, cf. Emery and Hamilton 1985, Mysak 1986).

To test whether the first principle component was actually related to ENSO events, we computed lagged correlations between it and the Southern Oscillation Index (SOI), a primary indicator of ENSO events (Table 4). The results show that the first principal component is highly correlated with the Southern Oscillation Index during the previous winter. Also, in all but one instance (sea level height and spring SOI) the three oceanographic variables are correlated with SOI in the previous winter in the way that would be expected from their loading in the first principle component.

To further simplify interpretation, we attempted to use a single indicator of abundance. In correlations computed thus far, no single population variable had a demonstrably stronger relationship to environmental variables tested. We therefore used the sum of commercial catch, recreational catch, and spawner estimates as a single indicator of annual population abundance. For the corresponding deconvolved estimate we use the deconvolution of this combination of these three series, the deconvolution that was previously shown to provide the best estimate of recruitment (Kope and Botsford 1988).

The results using the first principle component and the total abundance estimate (Table 5) indicate an influence of ENSO-related conditions during the summer of the third year ($\alpha \leqslant 0.05$) and provide weak evidence for an influence of ENSO-related conditions during the first spring ($\alpha \leqslant 0.10$). These relationships are reflected in both the total abundance and the estimate of recruitment to total abundance obtained through deconvolution. The estimate of total abundance is also correlated with previously identified oceanographic variables. The correlations with spring upwelling are -0.478 ($\alpha \leqslant 0.10$) and -0.511 ($\alpha \leqslant 0.01$) for total abundance and deconvolved total abundance, respectively. The correlations with summer ocean temperature are -0.551 ($\alpha \leqslant 0.10$) and -0.540 ($\alpha \leqslant 0.05$) for total abundance and deconvolved total abundance respectively.

Discussion

The negative correlation between abundance in the third year and the first principle component of the oceanographic variables is consistent with observed effects of ENSO events on coastal oceanographic conditions and fish populations. Productivity in the California Current, as represented by zooplankton biomass, has long been known to be inversely correlated with sea surface temperature (Reid et al. 1958, Reid 1962). High productivity has traditionally been attributed to upwelling, but this explanation was recently questioned by Chelton et al. (1982) who proposed that higher zooplankton biomass resulted from increased equatorward flow in the California Current. The two proposed mechanisms are difficult to separate because conditions conducive to upwelling would also increase the strength of the California Current. However, whether colder water comes from the subarctic or from deeper coastal waters, it is higher in nutrients than the warmer surface waters, hence colder ocean temperatures in the winter and spring are associated with higher productivity in the California current (Chelton et al. 1982). Effects on productivity would be most noticeable during strong ENSO events. For example, total catch and average weight of chinook salmon landed in the commercial and sport fisheries were lower during the recent 1983 ENSO event (PFMC 1984, Pearcy et al. 1985, Johnson 1988).

The weak correlation between marine environmental variables during the first summer and indices of abundance and recruitment is of the opposite sign to that expected on the basis of these relationships between the environment and productivity. However, it is possible that because juvenile fish feed on different prey than adult fish, shifts in prey distributions in warm-water years may result in higher growth and survival rates for juveniles. Northward shifts in the distribution of larval clupeids have been documented in warm-water years (Radovich 1959, 1961), and larval anchovies were found closer to shore than usual during the 1983 ENSO (Brodeur et al. 1985). Larval clupeids are a principal prey of juvenile chinook salmon (Peterson et al. 1982, Pearcy et al. 1985). Data taken off the Oregon coast show no significant difference in feeding by first-year chinook salmon between 1983, a warm-water year, and the other years 1980–85 (Brodeur and Pearcy In press).

The results obtained here for freshwater influences during the downstream migration in the first year have greater implications for the general methodology of correlation analysis in fisheries than for the dependence of salmon survival on environment. Other direct observations—the fact that differences in survival between marked fish released above the delta and marked fish released below the delta is correlated with flow over 10 years (USFWS 1987)—provide convincing evidence for a negative effect of low flows in the delta. Our results merely underscore the potential for falsely identifying a suspected relationship using standard methods for computing correlations. A dependence of abundance on freshwater variables was not detected when intraseries correlation was removed, rather than artificially added, and when it was taken into account in computing correlation coefficients. Fortunately, for this case there have been direct measurements of survival, and we need not rely solely on correlation analysis of abundance and environmental data.

Although a freshwater effect is not detectable in correlations with these freshwater variables, it may provide a partial explanation for the weak correlation seen between population variables and oceanographic conditions during the first year. During the spring, the first principle component of oceanographic variables is highly correlated with total delta inflow—flow in the Sacramento, Feather, and American Rivers (0.687, 0.577, 0.610, and 0.631, all significant at the 0.01 level using the conservative test). Thus the correlation between the first principle component of oceanographic variables during the first spring may be due to occurrences in freshwater, rather than oceanographic influences.

The various relationships implied in the results of this study provide a view of remote forcing of the North American marine and terrestrial environment that may be of general utility in examining the effects of environmental variability on other species. Events in the equatorial Pacific appear to drive the oceanographic and meteorological environment in the eastern North Pacific and western North America. Autocorrelations in the SOI (Table 4) indicate that the Equatorial events are spring to winter events (i.e., in column 1, seasons within any spring-to-winter period are correlated with each other, but none are correlated with seasons in any other spring-to-winter period). The rest of Table 4 indicates that these events influence conditions in our coastal ocean only in the following winter. This "winter only" aspect of this correlation is consistent with results relating an index of atmospheric pressure conditions on the west coast of North America, the Pacific North American index to events in the equatorial Pacific (Horel and Wallace 1981). Mysak (1986) attributed this "winter only" aspect of the equatorial/midlatitude teleconnection to the requirement for strong westerlies between the equator and midlatitudes in order to advect the atmospheric Rossby waves responsible for the teleconnection to the northeast. These westerlies exist only during the winter. The covariability among our three oceanographic variables (i.e., the fact that UPW is as important as SLH and SST in the loading on the first principle component) suggests an atmospheric teleconnection with equatorial ENSO rather than a wave propagating poleward from the Equator (cf. Emery and Hamilton 1985, Mysak 1986). These variables are also related to winter rainfall in central California. For example, annual rainfall in Sacramento is significantly correlated with the first principle component and the upwelling index in winter. Flows through the Sacramento-San Joaquin Delta the following spring are in turn correlated with that rainfall, as well as winter oceanographic conditions. This remote forcing on a global scale and the associated covariability of marine and terrestrial variables further confound the identification of causal mechanisms from these kinds of data.

However, even direct measures of survival versus environmental variables do not necessarily identify mechanisms unequivocally. Covariation between flow rates, diversions, and reversed flows in the lower San Joaquin River continue to obscure the true cause of lower run size in the San Joaquin River system (Kjelson and Brandes 1989, USFWS 1987).

The differences in results between standard methods and the new methods used here are a rough measure of how much more conservative they are. At the 0.10 level, for example, the more conservative method of computing the variance of the estimate of correlation coefficient yielded significant correlations roughly half as often as standard methods (Tables 1–3). These results, together with simulations that show that the combination of equations (1) and (2) yield the prescribed false detection rates (α) (Botsford and Wainwright unpubl.), imply that this correction for intraseries correlation or a similar one should be used in correlation analysis.

Deconvolution also reduced the number of significant correlations. For example, at the 0.10 level, using the standard test, there were only 6 significant correlations with deconvolved variables, whereas there were 21 significant correlations for corresponding variables that were not deconvolved. The fact that this ratio is lower when the more conservative correlated series test is used (5 with deconvolution and 13 without) is to be expected because the test itself accounts for some of the intraseries correlation. Although the number of significant correlations is less with deconvolution, we cannot recommend its use in all situations. Deconvolution can have two positive effects on correlation analysis: (1) It can provide a better estimate of recruitment, and (2) it can reduce intraseries correlation, hence the variance of the estimate of correlation coefficient (Kope and Botsford 1988). However it can also have a negative effect. If the deconvolution is marginally stable, the abundance data is noisy, or the coefficients of the deconvolution are inaccurate, deconvolution can lead to a poorer estimate of recruitment. In the results presented here, deconvolution introduced some additional significant correlations and reduced the magnitude of existing correlations (although they remained significant at the same level). This suggests that the deconvolved series may be a poorer proxy for recruitment than the raw abundance series, and that this detracts from the removal of intraseries correlation.

The practical implication for chinook salmon managers of the correlations obtained here is primarily a recommendation of where to focus further research rather than a means of immediately achieving a dramatic improvement in management. Because these stocks are managed by annually attempting to control effort based on an attempt to predict abundance, an understanding of the factors affecting abundance is necessary. The relationship between salmon populations and oceanographic conditions during the third year has an R^2 of 0.23, and hence would not produce predictions that could substantially improve catch. It also does not hold for oceanographic conditions in the previous 3-month period, hence there is little potential for long-term prediction. However, the results do indicate two potentially useful relationships between environment and abundance. Our understanding of these relationships could possibly be improved to the point that they could be useful in management. The ability to estimate numbers at each age in catch and escapement would improve our ability to determine potential oceanographic effects as well as provide a possible predictor of catch (i.e., 2-year olds). The current practice of differentiating jacks from older fish on the basis of size leads to considerable uncertainty that could be removed by determining age through hard parts or separation of modes in the size distributions each year. Also, the existence of a demonstrated freshwater effect implies we should attempt to remove that effect from the data before searching for an oceanographic effect. However, this is complicated by the fact that an unknown fraction of the annual catch is produced by hatchery fish that were trucked below the delta for release, and hence not exposed to that effect. Better knowledge of where and when fish are released could provide the basis for removal of the effects of variable release numbers and release strategies from the data before searching for oceanographic effects.

In general, results from correlation analyses in fisheries will always contain an element of doubt and, by themselves, are probably not strong enough evidence of causal relationships that management should be based on them. Poor performance of past relationships argue for less dependence on them (Sissenwine 1984, Drinkwater and Myers 1987, Walters and Collie 1988), however, as we have shown here, there are ways of improving the reliability of correlation analyses. For example, smoothing with moving averages should be done only when the level of measurement noise warrants it, and it should always be accompanied by some means of accounting for the intraseries correlation introduced. Although we agree that the resulting statistical relationships do not, by themselves, provide a solid basis for management, we are not as pessimistic as some others (e.g., Walters and Collie 1988) regarding the utility of correlation analysis. It supplies information on patterns that allows formulation of hypotheses that can then be tested through direct means. It increases the probability of detection of relationships that might otherwise be missed. Fisheries analysts cannot afford to dismiss the opportunities it provides, but should use it only as exploratory analysis (cf. Bakun 1990, Botsford et al. 1989).

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Citations

Bakun, A.

1975 Daily and weekly upwelling indices, west coast of North America, 1967–73. NOAA Tech. Rep. NMFS SSRF-693, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 114 p.

1990 L'oceans et la variabilité des populations marines. *In* Troadec, J.P. (ed.), L'homme et les écosystemes halieutiques, p. 155–187. Inst. Français Recherche Explor. Mer, Brest, France [in French].

Bartlett, M.S.

1946 On the theoretical specification and sampling properties of autocorrelated time series. J. R. Stat. Soc., B8:27–41.

Barton, A.C.K.

1980 Factors influencing the life history of spring Chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Columbia River watershed from 1960 to 1977. Ph.D. diss., Oregon State Univ., Corvallis, 243 p.

Bayley, G.V., and J.M. Hammersley

1946 The effective number of independent observations in an autocorrelated series. J. R. Stat. Soc., B8:184–197.

Botsford, L.W.

1986 Analysis of environmental influences on population dynamics. *In* Vincent, T.L., Y. Cohen, W.J. Grantham, G.P. Kirkwood, and J.M. Skowronski (eds.), Modeling and management of resources under uncertainty, Vol. 72 in Lecture Notes in Biomathematics, p. 54–64. Springer-Verlag, NY.

Botsford, L.W., D. Armstrong, and J.M. Shenker

1989 Oceanographic influences on the dynamics of commercially fished stocks. *In* Landry, M.R., and B. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 511–565. Elsevier Sci. Publ., Amsterdam.

Box, G.E.P., and G.M. Jenkins

1976 Time series analysis: Forecasting and control. Holden-Day, Oakland, 575 p.

Brodeur, R.D., and W.G. Pearcy

In press Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fish. Bull., U.S. 88(4).

Brodeur, R.D., D.M. Gadomski, W.G. Pearcy, H.P. Batchelder, and C.B. Miller

1985 Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Estuarine Coastal Shelf Sci. 2:365–378.

Cayan, D.R., and D.H. Peterson

1989 The influence of North Pacific atmospheric circulation on streamflow in the West. *In* Peterson, D.H. (ed.), Aspects of climate variability in the Pacific and the western Americas, p. 375–397. Geophys. Monogr. 55, Am. Geophys. Union, Wash. DC.

Chelton, D.B.

1984 Commentary: Short-term climatic variability in the northeast Pacific Ocean. *In* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 87–99. Oregon State Univ. Press, Corvallis.

Chelton, D.B., P.A. Bernal, and J.A. McGowan

1982 Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095–1125.

Denega, M.M.

1973 Age composition and growth rates of chinook salmon from northern California's salmon troll fishery. M.S. thesis, Humboldt State Univ., Arcata, CA, 56 p.

Dettman, D.H., and D.W. Kelley

1986 The roles of Nimbus hatchery and Fether River hatchery and natural reproduction in maintaining the lower American River salmon run. Report to the California Department of Water Resources by D.W. Kelley & Associates, Newcastle, CA, 73 p.

Dettman, D.H., D.W. Kelley, and W.T. Mitchell

1986 The influence of flow in Sacramento River salmon. Report to the California Department of Water Resources by D.W. Kelley & Associates, Newcastle, CA, 56 p.

Douglas, A.V., and P.J. Englehart

1981 On a statistical relationship between autumn rainfall in the central equatorial Pacific and subsequent winter precipitation in Florida. Monthly Weather Review 109:2377–2382.

Drinkwater, K.F., and R.A. Myers

1987 Testing predictions of marine fish and shellfish landings from environmental variables. Can. J. Fish. Aquat. Sci. 44: 1568–1573.

Emery, W.J., and K. Hamilton

1985 Atmospheric forcing of interannual variability in the northeast Pacific Ocean: Connections with El Niño. J. Geophys. Res. 90:857–868.

Enfield, D.B., and J.S. Allen

1980 On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. J. Phys. Oceanogr. 10:557–578.

Fogarty, M.J.

1988 Time series models of the Maine lobster fishery: The effect of temperature. Can. J. Fish. Aquat. Sci. 45:1145–1153.

Fry, D.H., Jr., and A. Petrovich, Jr.

1970 King salmon (*Oncorhynchus tshawytscha*) spawning stocks of the California Central Valley, 1963–1969. Admin. Rep. 70-11, Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 34 p.

Hallock, R.J.

1983 Effect of Red Bluff Diversion Dam on chinook salmon, *Oncorhynchus tshawytscha*, fingerlings. Calif. Dep. Fish Game, Red Bluff, CA, 8 p.

Hallock, R.J., and R.R. Reisenbichler

1979 Evaluation of returns of chinook salmon, *Oncorhynchus tshawytscha*, released as fingerlings at Coleman and Nimbus hatcheries and in the Sacramento River Estuary. Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 10 p.

Hallock, R.J., D.A. Vogel, and R.R. Reisenbichler

1982 The effect of Red Bluff Diversion Dam on the migration of adult chinook salmon, *Oncorhynchus tshawytscha*, as indicated radio-tagged fish. Admin. Rep 82-2, Calif. Dep. Fish Game, Anad. Fish. Branch, Rancho Cordova, CA, 47 p.

Harris, R.J.

1975 A primer of multivariate statistics. Acad. Press, NY, 332 p.

Hickey, B.M.

1989 Patterns and processes of circulation over the Washington Continental shelf and slope. Chapter 3. *In* Landry, M.R., and B. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 41–115. Elsevier Sci. Publ., Amsterdam.

Hollowed, A.B., K.M. Bailey, and W.S. Wooster

1987 Patterns in recruitment of marine fishes in the northeast Pacific ocean. Biol. Oceanogr. 5:99–131.

Horel, J.D., and J.M. Wallace

1981 Planetary-scale atmospheric phenomena associated with the Southern Oscillation. Monthly Weather Review 109: 813–829.

Johnson, S.L.
1988 The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fish. Res. 6:105–123.

Kjelson, M.A., and P.L. Brandes
1989 The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento-San Joaquin rivers, California. *In* Levins, C.D., L.B. Holtby, and M.A. Henderson (eds.), Proceedings, National workshop on the effects of habitat alteration on salmonid stocks, p. 100–115. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Kjelson, M.A., P.F. Raquel, and F.W. Fisher
1981 Influences of freshwater inflow on chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin Estuary. *In* Cross, R.D., and D.L. Williams (eds.), Proceedings, National symposium on freshwater inflow to estuaries, p. 88–104. U.S. Fish Wildl. Serv., Office Biol. Serv. FWS/OBS-81/04.

Kope, R.G.
1987 Separable virtual population analysis of Pacific salmon with application to marked chinook salmon, *Oncorhynchus tshawytscha*, from California's Central Valley. Can. J. Fish. Aquat. Sci. 44:1213–1220.
1988 Effects of initial conditions on Monte Carlo estimates of bias in estimating stock-recruitment relationships. Can. J. Fish. Aquat. Sci. 45:185–187.

Kope, R.G., and L.W. Botsford
1988 Detection of environmental influence on recruitment using abundance data. Can. J. Fish. Aquat. Sci. 45:1448–1458.

Markham, C.G., and D.R. McLain
1977 Pacific sea-surface temperature related to rain in California. Nature (Lond.) 269:502–504.

Mysak, L.A.
1986 El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464–497.

Norton, J.G.
1987 Ocean climate influences on rockfish recruitment in the California Current. *In* Proceedings, International Rockfish Symposium, 20–22 Oct. 1986, Anchorage, Alaska, p. 73–98. Alaska Sea Grant Rep. 87-2, Univ. Alaska, Fairbanks.

PFMC (Pacific Fishery Management Council)
1984 A review of the 1983 ocean salmon fisheries and status of stocks and management goals for the 1984 salmon season off the coasts of California, Oregon, and Washington. Pac. Fish. Manage. Counc., Portland, OR 97201, 218 p.

Pearcy, W., J. Fisher, R. Brodeur, and S. Johnson
1985 Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 188–204. Wash. Sea Grant Prog., Univ. Wash., Seattle, 312 p.

Peterson, W.T., R.D. Brodeur, and W.C. Pearcy
1982 Food habits of juvenile salmon in the Oregon coastal zone, June 1979. Fish. Bull., U.S. 80:841–851.

Radovich, J.
1959 Redistribution of fishes in the eastern North Pacific Ocean in 1957 and 1958. Calif. Coop. Oceanic Fish. Invest. Rep. 3:163–171.
1961 Relationships of some marine organisms of the Northeast Pacific to water temperatures, particularly during 1957 through 1959. Calif. Dep. Fish Game, Fish. Bull. 112, 62 p.

Redmond, K.
1988 Surface temperature and precipitation variations in the western U.S. and their relation to large scale circulation indices. *In* Fifth Workshop on Climate Variability of the Eastern North Pacific and Western North America, Pacific Grove, CA, p. 15–16. Sponsored jointly by Natl. Science Foundation, Monterey Bay Aquarium Research Inst., and the U.S. Geological Survey.

Reid, J.L.
1962 On the circulation, phosphate-phosphorous content and zooplankton volume in the upper part of the Pacific Ocean. Limnol. Oceanogr. 7:287–306.

Reid, J.L., G.I. Roden, and J.G. Wyllie
1958 Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 5:28–57.

Reisenbichler, R.R.
1986 Use of spawner-recruit relations to evaluate the effect of degraded environment and increased fishing on the abundance of fall-run chinook salmon, *Oncorhynchus tshawytscha*, in several California streams. Ph.D. diss., Univ. Wash., Seattle, 175 p.

Sholes, W.H., and R.J. Hallock
1979 An evaluation of rearing fall-run chinook salmon, *Oncorhynchus tshawytscha*, to yearlings at Feather River Hatchery with comparison of returns from hatchery and downstream releases. Calif. Fish Game 65:239–255.

Sissenwine, M.P.
1984 Why do fish populations vary? *In* May, R.M. (ed.), Exploitation of marine communities, p. 59–94. Springer-Verlag, NY.

Stevens, D.E., and L.W. Miller
1983 Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt and delta smelt in the Sacramento-San Joaquin River system. N. Am. J. Fish. Manage. 3:425–437.

Sutcliffe, W.H., Jr., R.H. Loucks, and K.F. Drinkwater
1976 Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33:98–115.

USFWS
1987 The needs of chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento-San Joaquin estuary. Exhibit 31, entered by the U.S. Fish and Wildlife Service for the State Water Resources Control Board. 1987 Water Quality/Water Rights Proceeding on the San Francisco Bay/Sacramento-San Joaquin Delta. Bay-Delta Project, U.S. Fish. Wildl. Serv., Stockton, CA 95205, 179 p.

Van Hyning, J.M.
1973 Factors affecting the abundance of fall chinook salmon in the Columbia River. Oreg. Fish Comm. Res. Rep. 4, 87 p.

Walters, C.J.
1985 Bias in the estimation of functional relationships. Can. J. Fish. Aquat. Sci. 42:147–149.

Walters, C.J., and J.S. Collie
1988 Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45:1848–1854.

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SEX DETERMINATION OF THE CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS CALIFORNIANUS*) FROM CANINE TEETH

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Abstract

Size of canine teeth from California sea lion (*Zalophus californianus californianus*) carcasses is shown to be useful in determining the sex of animals which have missing genitalia or which are otherwise of unknown sex. A total of 267 canine teeth from carcasses of 68 males and 43 females were measured along five axes. Of root and crown measurements of upper and lower canines, males and females overlapped only in root thickness of upper canines. A multivariate ANOVA showed a significant difference in the size of canines between upper and lower canines, and between males and females. Stepwise discriminant analysis produced discriminant functions for upper and lower canines for determining sex of unknown-sexed California sea lions. A separate set of canine teeth from 39 male and 49 female California sea lions was correctly classified without prior knowledge of sex by visual inspection and by the two discriminant functions.

Key words: California sea lion, *Zalophus californianus,* sex determination, canine teeth.

Sex determination from genitalia is often not possible when soft tissue is badly decomposed. While extracting canine teeth from carcasses of California sea lions (*Zalophus californianus californianus*) to obtain age information, we noted size differences between canines of males and females, and that the size of the crown remained constant through life for each sex (Fig. 1). Other researchers have reported the use of canine or skull measurements for determining sex of other carnivores (Crespo 1984, Fuller *et al.* 1984, Parson *et al.* 1978, Sauer 1966, Flook and Rimmer 1965). In this report, we evaluate canine tooth size as an indicator of sex of California sea lions.

Materials and Methods

Several researchers (see Acknowledgments) collected carcasses of California sea lions of various ages and known sex from (1) coastal mainland beaches of

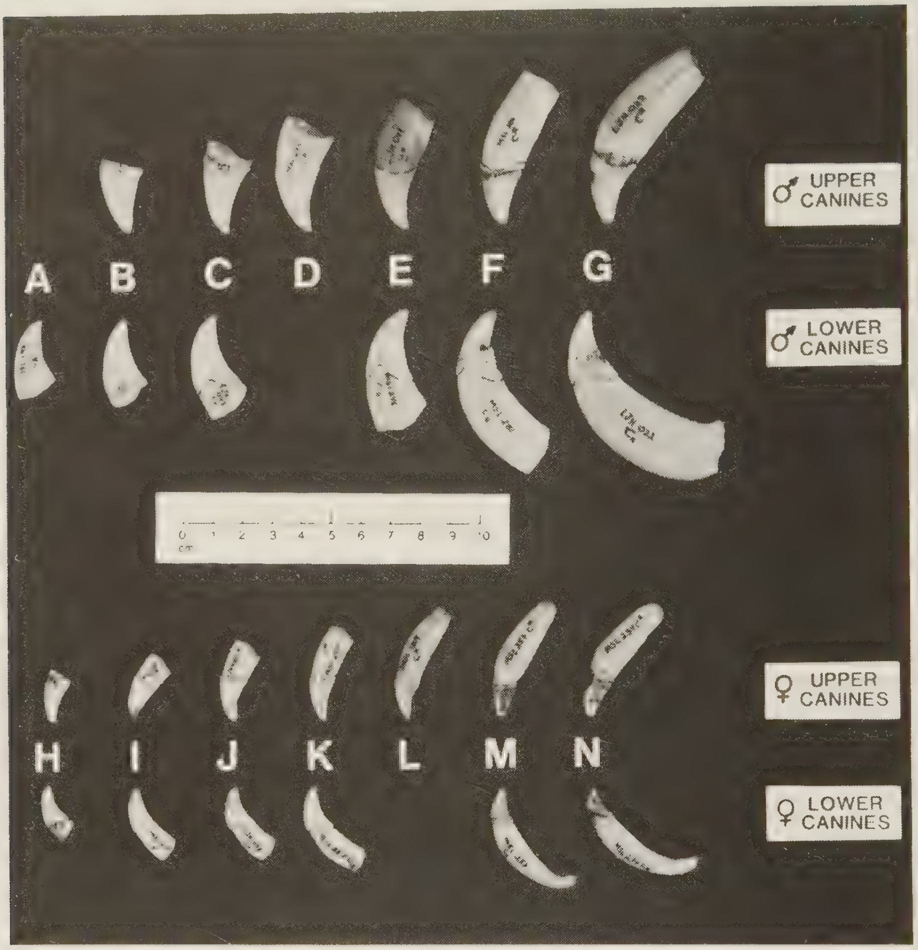

Figure 1. Ontogenetic series of upper and lower canine teeth from known-sex California sea lions (*Zalophus californianus californianus*). The estimated age and standard length of each specimen are: A (5 mo, 87 cm); B (7 mo, 91 cm); C (11 mo, 130 cm); D (2 yr, 145 cm); E (4 yr, 165 cm); F (7 yr, 186 cm); G (12 yr, 232 cm); H (4 mo, 80 cm); I (7 mo, 99 cm); J (11 mo, 116 cm); K (2 yr, 132 cm); L (6 yr, 152 cm); M (10 yr, 165 cm); and N (12 yr, 180 cm).

San Diego County, California; (2) San Clemente, Santa Catalina, and San Nicolas islands, California; (3) Bolsa Chica State Beach, Orange County, California; (4) Farallon Islands, California; and (5) vessels at sea which caught the animals inadvertently during fishing operations. All canines present on the carcass were extracted and the dental position was noted as upper right or left, or, lower right or left. We collected 267 canines from carcasses of 68 males and 43 females.

A sub-sample of canines from various age and length classes of California sea lions was photographed to demonstrate that there is a distinct difference in the size of the canines between males and females (Fig. 1). Ages of sea lions from this sub-sample were either known (animals had been tagged as pups at San Clemente and San Nicolas Islands) or estimated by reading layers from an acid-etched canine from the same animal (Pierce and Kajimura 1980). Counts of dentine growth layer groups (GLG's), as defined by Myrick (1980), were made to estimate age of animals greater than 1 yr old. The deposition rate of GLG's was calibrated from a canine of a captive California sea lion known to be 12 yr old and from sea lions tagged in the wild as pups. Each GLG was found to represent one year. For animals less than 1 yr, an approximate age was determined by taking the difference between the specimen collection date and end of the pupping period, which takes place during the last week of June (Odell 1975).

Canines were used for sex determination only if the crown was completely developed. This criterion eliminates animals which are too young for the tooth measurements to be effective in distinguishing the sex of the animal. We estimate that this criterion will be met at approximately five to six months of age for males and as early as three to four months of age for females. The canine from the youngest sea lion male (specimen A in Fig. 1) was collected from a 5-month-old animal. The lower canine from this young male specimen has a crown that is almost fully developed and with signs of a developing root. A canine from the youngest female specimen (specimen H in Fig. 1) was collected from a 4-month-old animal. The crowns of the upper and lower canines are fully developed and the root has formed in this female.

The canines of pup and juvenile sea lions must be removed from the skull or mandible to determine relative size of the teeth because part of the crown remains embedded in the alveolus. The discolored region evident on the apex of the canines shown in Figure 2 denotes the exposed portion of the fully developed crown of canines from a pup.

All canines collected were measured along five axes. We measured (±0.01 mm) (1) crown length of upper and lower canines in a straight line from the concave side of the canine (posteriorly) from the neck to apex, (2) crown width and (3) thickness at the widest region of the neck or base of the crown, and (4) root width and (5) thickness at the root's widest and thickest region, respectively (Fig. 3). Some measurements of individual canine teeth were excluded because: (1) the crown was excessively worn (in one animal the crown was flat and level with the gum line); (2) the canine had been sectioned for age determination before all measurements were obtained; and/or (3) the root had not developed (in newborn pups only).

Before testing for sex-related differences we tested for dental-position differences in the measurements taken of each canine for all four dental positions (upper and lower; right and left). Only canines measured at the five previously mentioned locations of the tooth were used. The effect of dental position and sex were tested using MANOVA (Program 4V of BMDP-88; Dixon 1988). Multiple univarite ANOVA's were not used because multiple measurements from the same tooth could not be considered independent.

We also performed stepwise discriminant analysis (Program 7M of BMDP-87; Dixon 1985) to produce a discriminant score function to ascertain the sex

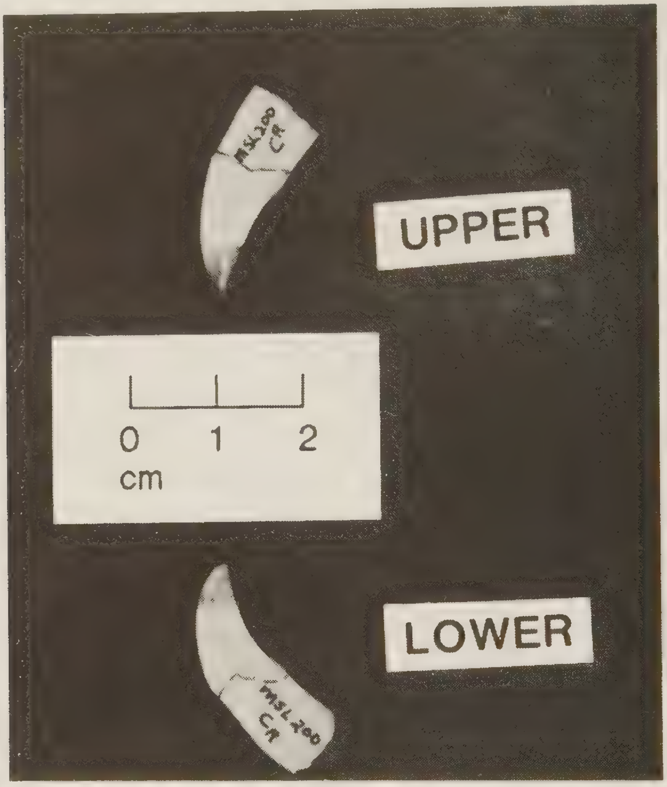

Figure 2. Canine teeth from an approximately 7-mo-old female California sea lion (*Zalophus californianus californianus*) showing exposed region (discoloration) at the apex of a fully developed crown.

of a California sea lion based on the canine measurements performed on any of four canines. This analysis was made because root thickness of upper canines overlapped between sex, and we did not know if other measurements would overlap if a larger sample size was available.

Without knowledge of sex, a second set of canines taken from 39 male and 49 female California sea lions collected from San Miguel Island, California was used to test the two functions and to determine if sex could be determined by visual examination of the canines. For the visual discrimination test, the teeth were examined visually before any measurements taken and separated into male and female. To test the two functions, the teeth were measured along the five axes and the two measurements chosen by stepwise discriminant analysis were used to identify male and female.

Results

Of root and crown measurements of upper and lower canines, males and females overlapped only in root thickness of upper canines (Table 1). For each sex we rejected the hypothesis that mean canine measurement vectors were equal

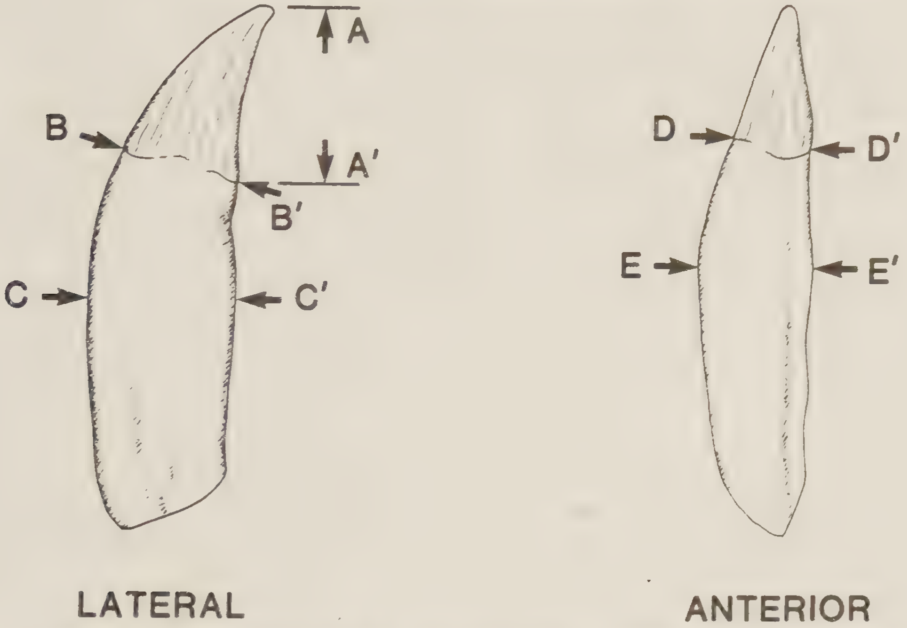

Figure 3. Measurements taken of California sea lion (*Zalophus californianus californianus*) canine teeth (A–A′ = crown length; B–B′ = crown width; C–C′ = root width; D–D′ = crown thickness; and E–E′ = root thickness).

for upper and lower dental positions ($P < 0.01$), but did not reject the hypothesis of equal right and left dental-position ($P \geq 0.66$). For upper and lower canine positions, we rejected the hypothesis that mean canine measurement vectors are equal for males and females ($P < 0.01$, in each case).

Upper and lower canines were used in two separate stepwise discriminant analysis tests because a significant difference was found between those dental

Table 1. The sample size and range of measurements (mm) for 267 sampled canine teeth taken from known-sex California sea lions (*Zalophus californianus californianus*).

		Female			Male		
Position of canine	Measurement	*n*	Minimum	Maximum	*n*	Minimum	Maximum
Upper	Crown length	49	12.44	16.44	60	19.24	24.74
	Crown width	52	6.36	9.75	70	11.09	15.89
	Crown thickness	51	4.07	7.66	67	8.15	11.95
	Root width	58	8.17	12.40	73	13.78	22.85
	Root thickness	58	5.64	10.42	73	10.41	16.19
Lower	Crown length	54	10.97	14.96	81	17.76	27.26
	Crown width	54	6.03	9.81	84	11.10	17.08
	Crown thickness	54	3.84	6.18	84	7.00	10.47
	Root width	52	7.45	11.40	79	12.35	22.28
	Root thickness	52	4.50	7.52	78	8.06	18.30

positions, and not for left and right dental positions. After stepwise discriminant analysis of upper canines was made, root thickness of lower canines was eliminated from the analysis in order to have the same measures for the two dental positions. Each stepwise discriminant analysis chose root width and crown length as two measurements used in the discriminant function for determining sex of California sea lions from one of their canine teeth. A 100% jackknifed classification was achieved for upper canines of 57 males and 48 females, and for lower canines of 76 males and 51 females. The discriminant function for upper canines is:

$$S = 0.33763x + 0.67752y - 17.20254 \tag{1}$$

The discriminant function for lower canines is:

$$S = 0.30240x + 0.59720y - 15.91558 \tag{2}$$

where x = root width, and y = crown length, and S is the discriminant score. If the discriminant score (S) for upper canines is greater than -0.31707, then the canine is from a male; if it is less, then it is from a female. If the discriminant score for lower canines is greater than -0.85475, then the canine is from a male; if it is less, then it is from a female.

Without prior knowledge of sex, a 100% accuracy rate was achieved in identifying the sex of 39 male and 49 female California sea lions. These animals were correctly sexed without any measurements by visually discriminating between the two different sizes of canines. They were also correctly sexed by using measurements of root width and crown length with the discriminant functions. Although crown length is affected in older animals by wear (*i.e.*, the point of the crown is rounded), we found that the formulas correctly determined the sex of animals with this condition.

Discussion

Our results indicate that California sea lions can be sexed by examination of any of their canines. This difference is obvious enough that sex can be accurately determined from visual inspection of a canine. If the identification is in doubt, we have provided two formulas (one for upper canines and one for lower canines) for determining the sex of California sea lions from two measurements of a canine. Unless crown length is abnormally worn, the two formulas should identify the sex of the sea lion. For animals with abnormally worn crowns, we suggest comparing the other measurements to those found in Table 1 to determine the sex of these animals.

This technique may be of use in determining the sex of decomposed or mummified carcasses of other sexually dimorphic pinnipeds such as the Guadalupe fur seal (*Arctocephalus townsendi*), northern fur seal (*Callorhinus ursinus*), northern (Steller) sea lion (*Eumetopias jubatus*), and northern elephant seal (*Mirounga angustirostris*). Possible applications of this technique would be to determine the sex ratio of dead pups and juveniles in rookeries, or to increase the sample size of known-sexed animals for age-determination studies.

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LITERATURE CITED

CRESPO, E. A. 1984. Dimorfismo sexual en los dientes caninos y en los craneos del lobo marino del sur, *Otaria flavescens* (Shaw) (Pinnipedia, Otariidae). Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigacion de las Ciencias Naturales, Zoologia 9:245–254.

DIXON, W. J. 1985. BMDP statistical software. BMDP 1987 IBM-PC program version. University of California Press. Berkeley, CA.

DIXON, W. J. 1988. BMDP statistical software. University of California Press. Berkeley, CA.

FLOOK, D. R., AND J. RIMMER. 1965. Cannibalism in starving wolverines and sex identification from skulls. Canadian Field Naturalist 79:171–173.

FULLER, T. K., D. P. HOBSON, J. R. GUNSON, D. B. SCHOWALTER AND D. HEISEY. 1984. Sexual dimorphism in mandibular canines of striped skunks. Journal of Wildlife Management 48:1444–1446.

MYRICK, A. C., Jr. 1980. Report of the workshop: Section G, Glossary. Pages 48–50 *in* W. F. Perrin and A. C. Myrick, eds. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue 3.

ODELL, D. K. 1975. Breeding biology of the California sea lion (*Zalophus californianus*). Rapports et Procès-verbeaux des Réunions Conscil International pour l'Exploration de la Mer 169:374–378.

PARSON, G. R., M. K. BROWN and G. B. WILL. 1978. Determining the sex of fisher from the lower canine teeth. New York Fish & Game Journal 25:42–44.

PIERCE, K. V., AND H. KAJIMURA. 1980. Acid etching and highlighting for defining growth layers in cetacean teeth. Pages 99–103 *in* W. F. Perrin and A. C. Myrick, eds. Age determination of toothed whales and sirenians. Reports of the International Whaling Commission, Special Issue 3.

SAUER, P. R. 1966. Determining sex of black bear from the size of the lower canine tooth. New York Fish & Game Journal 13:140–145.

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Food Habits of California Sea Lions *Zalophus californianus* at San Clemente Island, California, 1981–86

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Abstract.–We studied the food habits of the California sea lion *Zalophus californianus* at San Clemente Island, California, from September 1981 through September 1986 using fish otoliths, cephalopod beaks, and other prey remains we recovered from 1476 fecal samples (i.e., scats). We identified 44 types of prey to species and 8 types of prey to genus. Seven types of prey occurred in at least 10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). We examined trends in the occurrence of these seven species and of Pacific mackerel *Scomber japonicus* and octopus (*Octopus* spp.) in scats of California sea lions. We found significant differences among seasons and years, and season-year differences in the occurrence of northern anchovy, jack mackerel, Pacific whiting, and octopus ($P \leq 0.01$). Significant effects due to year and season-year interaction were found for pelagic red crab, rockfish, market squid, and blacksmith. Pacific mackerel showed a significant difference only among years. Significant differences in the occurrence of Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus, and pelagic red crab ($P<0.01$) were found during pre-El Niño, El Niño, and post-El Niño periods.

Knowledge of California sea lion *Zalophus californianus* food habits in the Southern California Bight (SCB, Fig. 1) has come from stomach content analysis by Scheffer and Neff (1948), and Fiscus and Baines (1966); and from the 1978–79 spring and summer study at San Miguel Island from scat (i.e., fecal) analysis by Antonelis et al. (1984). These studies identified a wide variety of prey. Antonelis et al. (1984) reported that Pacific whiting, market squid, juvenile rockfish, and northern anchovy were the four most important prey at San Miguel Island. A 4-year study at the Farallon Islands in northern California (outside the breeding area) found that sea lions switched between Pacific whiting and juvenile rockfish (Bailey and Ainley 1982).

From 1981 to 1986, we examined prey consumed by California sea lions using the shoreline located at and south of Mail Point, San Clemente Island (SCI, Fig. 1). San Clemente Island has one of the smallest rookeries in the SCB (producing approximately 666 pups in 1981) as compared with San Miguel and San Nicolas islands (producing approximately 8255 and 6704 pups, respectively, in 1981; DeMaster et al. 1982, Stewart and Yochem 1984, Oliver and Lowry 1987). We analyzed fecal samples (scats) to identify prey composition and temporal changes in the diet. This period was characterized by an abnormal influx of warm water into the SCB during the 1982–83 El Niño/Southern Oscillation (McGowan 1984). Effects of this El Niño within the SCB became evident in October 1982, when sea-surface temperatures were 1–2°C above normal, and zooplankton levels declined (McGowan 1984). Water temperatures returned to normal in October–November 1984 (F. Miller, Inter-Am. Trop. Tuna Comm., La Jolla, CA 92038, pers. commun., Oct. 1986). This warm-water period off California has been referred to as the California El Niño (McGowan 1984, Fiedler et al. 1986).

Methods

Sample collection

We collected fresh and dry scats during 40 trips to SCI with between-trip intervals ranging from 2 weeks to 3 months. Scats were separated into one of three categories: (1) fresh

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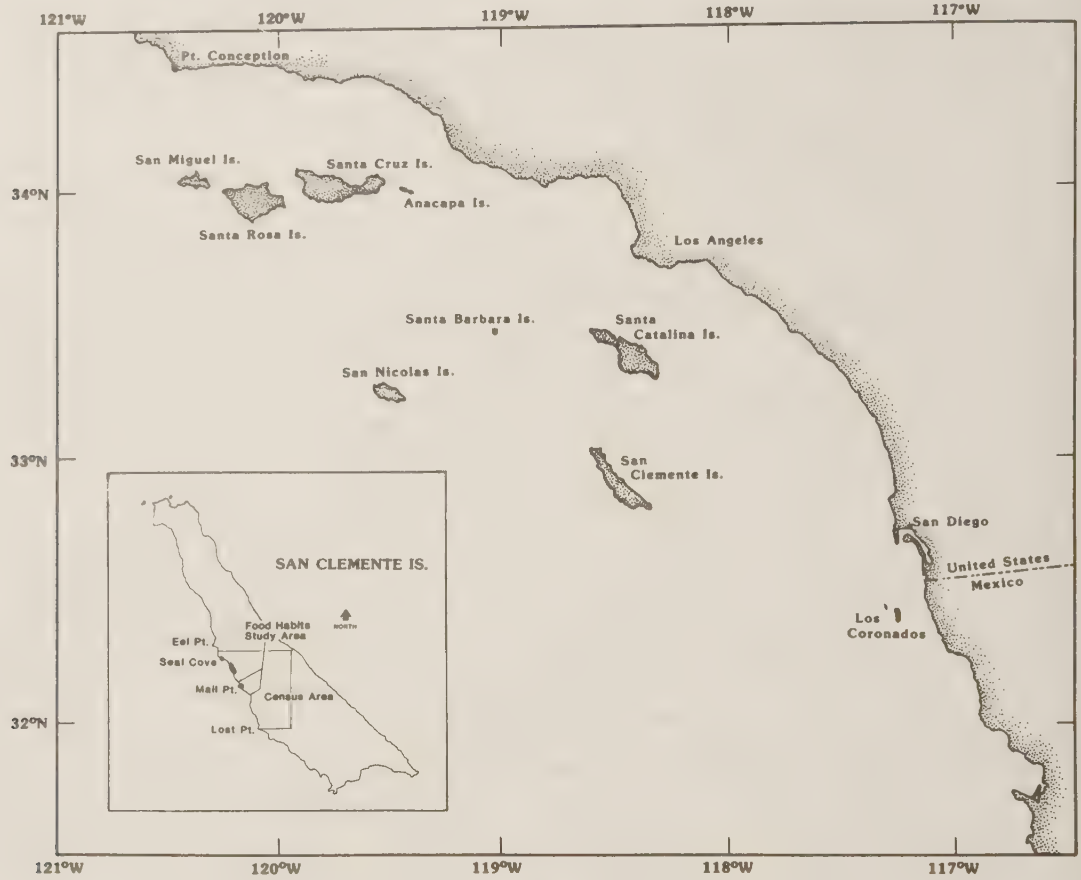
121°W
120°W
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118°W
117°W
34°N
33°N
32°N
Pt. Conception
San Miguel Is.
Santa Cruz Is.
Anacapa Is.
Santa Rosa Is.
Los Angeles
Santa Barbara Is.
Santa Catalina Is.
San Nicolas Is.
San Clemente Is.
San Diego
United States
Mexico
Los Coronados
SAN CLEMENTE IS.
Food Habits Study Area
NORTH
Eel Pt.
Seal Cove
Mail Pt.
Census Area
Lost Pt.

Figure 1
Map showing Southern California Bight (SCB) and San Clemente Island (SCI).

scats, (2) dried scats representing one between-trip interval, and (3) dried scats representing more than one between-trip interval. Fresh scat samples represented the diet of sea lions within 3 to 4 days of the collection. The second category provided dietary information from the previous scat collection period to the time represented by fresh scats. The third category represented a much longer period.

Each scat was placed in a plastic bag, stored in an air-tight plastic container, and frozen until processed. Scats were soaked in a mild soap solution for 1–5 days, and then rinsed with water through two or three nested sieves. During September 1981–March 1983 we used three sieves (mesh sizes 2.8 mm, 1.5 mm, and 1.00 mm) and during April 1983–September 1986 we used two sieves (mesh sizes 2.8 mm and 0.710 mm). After rinsing, we collected fish otoliths, cephalopod beaks, shark teeth, and cartilaginous vertebrae. Otoliths, shark teeth, and cartilaginous vertebrae were air dried and stored in gelatin capsules; cephalopod beaks were stored in vials containing 70% ethanol. We noted the presence or absence of fragments of pelagic red crabs *Pleuroncodes planipes*.

Sample analysis

Prey items were identified to the lowest taxon possible from comparative specimens and drawings (Iverson and Pinkas 1971, Eschmeyer et al. 1983). We used sagittal otoliths to identify teleost fishes, cephalopod beaks to identify squid and octopus, teeth to identify elasmobranchs, and exoskeletal fragments to identify pelagic red crabs. We counted left and right sagittal otoliths, and upper and lower cephalopod beaks.

Table 1

California sea lion *Zalophus californianus* scat samples collected seasonally from San Clemente Island, California, 1981–86.

			Number of scats collected			
				Dry		
Year	Season	Number of collection trips	Fresh	1 between-trip interval	>1 between-trip interval	Total collected
1981	Autumn	3	22	19	7	48
1981–82	Winter	1	0	3	0	3
1982	Spring	4	27	80	52	159
1982	Summer	4	76	67	7	150
1982	Autumn	1	1	53	0	54
1982–83	Winter	2	3	56	0	59
1983	Spring	3	37	73	60	170
1983	Summer	2	6	71	10	87
1983	Autumn	1	22	56	17	95
1983–84	Winter	3	93	51	4	148
1984	Spring	2	81	20	16	117
1984	Summer	3	88	1	0	89
1984	Autumn	2	13	40	0	53
1984–85	Winter	1	0	16	0	16
1985	Spring	1	11	1	0	12
1985	Summer	2	60	0	0	60
1985	Autumn	1	25	0	0	25
1986	Spring	1	44	0	0	44
1986	Summer	2	65	0	0	65
1986	Autumn	1	22	0	0	22
Total		40	696	607	173	1476

We used indices of occurrence, composition, and number to quantify prey taxon consumed by sea lions. Only scat samples containing otoliths, cephalopod beaks, shark teeth, cartilaginous vertebrae, or pelagic red crab fragments were used in the analysis. The occurrence index, or percent occurrence (PO), is a measure of the percentage of scat samples in which a prey taxon occurred. The composition index, or percent prey composition (PPC), is a measure of the percentage of occurrences for each prey taxon from a tally of occurrences from all prey taxa found in a group of samples. The number index, or percent minimum number (PMN), measures the percentage of numbers of individual prey taxon. To compute the number index, we used the maximum count of either left or right otoliths, or upper or lower beaks, which represent the minimum number of individual prey taxon. The counts for all prey taxa are summed and the percentage of each prey taxon is determined from the sum of all counts. The number index is, then, the percentage represented by each prey taxon from the sum of all maximum counts taken of all prey taxa found in a group of samples.

Interpretation of the number index is limited because it excludes (1) all prey hard parts found that were broken or digested, and not categorized as either left or right otoliths or upper or lower beaks, and (2) prey that lacked otoliths or beaks (e.g., pelagic red crabs and sharks). However, we think that this index is useful because fish and cephalopods represented the majority of prey in scat samples.

Percent occurrence indicates prey consumption without regard to other prey, and may indicate temporal availability, selectivity, or ease of capture of individual prey. Percent prey composition indicates the relative proportions of prey consumed. Percent minimum number of prey indicates numbers of prey consumed and is an index of the rate of consumption of individual prey.

Statistical analysis

We used all scats to determine what prey taxa were consumed, and then limited our examination of temporal variations in prey consumption to prey that occurred in at least 10% of these scats, were found in at least 80% of the seasons, or were occasionally very abundant. Only fresh scats and dried scats representing one between-trip interval were used in the temporal analyses of sea lion diets. We combined the 40 collection trips (Table 1) by season into winter (December–

Table 2

Number of prey occurrences (*n* Occur), percent occurrence (PO), percent prey composition (PPC), minimum number of individual prey (*n* Ind.), and percent minimum number (PMN) of prey found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86.

Prey						
Scientific name	Common name	*n* Occur	PO	PPC	*n* Ind.	PMN
Engraulis mordax	northern anchovy	672	51.3	24.7	9,398	54.4
Trachurus symmetricus	jack mackerel	322	24.6	11.8	1,220	7.1
Pleuroncodes planipes *	pelagic red crab	277	21.2	10.2	—**	—
Merluccius productus	Pacific whiting	256	19.6	9.4	2,110	12.2
Sebastes spp.	rockfish	249	19.0	9.2	1,245	7.2
Loligo opalescens	market squid	214	16.3	7.9	1,516	8.8
Chromis punctipinnis *	blacksmith	140	10.7	5.1	580	3.4
Scomber japonicus	Pacific mackerel	125	9.5	4.6	215	1.2
Octopus spp.	octopus	67	5.1	2.5	523	3.0
Onychoteuthis borealijaponicus	squid	39	2.2	1.1	33	<0.5
Lyopsetta exilis	slender sole	11	0.8	<0.5	19	<0.5
Oxyjulis californica *	señorita	14	1.1	0.5	20	<0.5
Porichthys notatus	plainfin midshipman	9	0.7	<0.5	11	<0.5
Abraliopsis spp.*	squid	9	0.7	<0.5	11	<0.5
Gonatus spp.	squid	9	0.7	<0.5	11	<0.5
Lycodes cortezianus *	bigfin eelpout	7	0.5	<0.5	8	<0.5
Sebastolobus alascanus *	shortspine thornyhead	6	0.5	<0.5	7	<0.5
Microstomus pacificus	dover sole	6	0.5	<0.5	8	<0.5
Glyptocephalus zachirus	rex sole	6	0.5	<0.5	7	<0.5
Icichthys lockingtoni	medusafish	5	<0.5	<0.5	7	<0.5
Xeneretmus ritteri *	stripefin poacher	3	<0.5	<0.5	5	<0.5
Citharichthys sordidus	Pacific sanddab	4	<0.5	<0.5	5	<0.5
Atherinops affinis *	topsmelt	3	<0.5	<0.5	4	<0.5
Semicossyphus pulcher *	sheephead	3	<0.5	<0.5	3	<0.5
Seriphus politus	queenfish	2	<0.5	<0.5	26	<0.5
Cypselurus californicus *	California flying fish	2	<0.5	<0.5	8	<0.5
Genyonemus lineatus	white croaker	2	<0.5	<0.5	6	<0.5
Galeorhinus zyopterus *	soupfin shark	2	<0.5	<0.5	—	—
Symbolophorus californiensis	California lanternfish	2	<0.5	<0.5	2	<0.5
Paralabrax clathratus *	kelp bass	2	<0.5	<0.5	2	<0.5
Chilara taylori	spotted cusk-eel	2	<0.5	<0.5	2	<0.5
Cymmatogaster aggregata	shiner surfperch	2	<0.5	<0.5	2	<0.5
Stenobrachius leucopsarus	northern lampfish	2	<0.5	<0.5	2	<0.5
Paralabrax sp.*	seabass	1	<0.5	<0.5	3	<0.5
Ocythoe tuberculata *	squid	1	<0.5	<0.5	2	<0.5
Girella nigricans	opaleye	1	<0.5	<0.5	2	<0.5
Zalembius rosaceus	pink surfperch	1	<0.5	<0.5	1	<0.5
Zaniolepis sp.*	combfish	1	<0.5	<0.5	1	<0.5
Xeneretmus sp.*	poacher	1	<0.5	<0.5	1	<0.5
Prionace glauca *	blue shark	1	<0.5	<0.5	—	—
Argentina sialis *	Pacific argentine	1	<0.5	<0.5	1	<0.5
Hippoglossina stomata *	bigmouth sole	1	<0.5	<0.5	1	<0.5
Parophrys vetulus	english sole	1	<0.5	<0.5	1	<0.5
Xeneretmus triacanthus *	bluespotted poacher	1	<0.5	<0.5	1	<0.5
Ceratoscopelus townsendi *	dogtooth lampfish	1	<0.5	<0.5	4	<0.5
Citharichthys sp.	sanddab	1	<0.5	<0.5	1	<0.5
Careproctus melanurus *	blacktail snailfish	1	<0.5	<0.5	1	<0.5
Medialuna californiensis *	halfmoon	1	<0.5	<0.5	3	<0.5
Synodus lucioceps *	California lizardfish	1	<0.5	<0.5	1	<0.5
Octopoteuthis deletron *	squid	1	<0.5	<0.5	1	<0.5
Unid. Myctophidae	lanternfish	17	1.3	0.6	29	<0.5
Unid. Embiotocidae	surfperch	4	<0.5	<0.5	7	<0.5
Unid. Atherinidae	silverside	3	<0.5	<0.5	3	<0.5
Unid. Labridae	wrasse	3	<0.5	<0.5	8	<0.5
Unid. Cottidae	sculpin	2	<0.5	<0.5	2	<0.5
Unid. Zoarcidae	eelpout	2	<0.5	<0.5	2	<0.5

Table 2 (continued)

Prey						
Scientific name	Common name	*n* Occur	PO	PPC	*n* Ind.	PMN
Unid. Gonatidae	squid	1	<0.5	<0.5	1	<0.5
Unid. Scombridae	mackerel or tuna	1	<0.5	<0.5	2	<0.5
	Unid. flatfish	5	<0.5	<0.5	6	<0.5
	Unid. cephalopod	31	2.4	1.1	19	<0.5
	Unid. cartilaginous fish	2	<0.5	<0.5	—	—
	Unid. fishes	83	6.3	3.1	62	<0.5

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*Not previously reported as prey of California sea lions.
**Data impossible to compute in fields marked with a dash (—).

February), spring (March–May), summer (June–August), and autumn (September–November). We also categorized our sample into three groups related to the California El Niño: (1) pre-El Niño (September 1981–August 1982), (2) El Niño (November 1982–September 1984), and (3) post-El Niño (November 1984–September 1986).

We tested for seasonal and yearly differences in presence or absence of each prey taxon using two-way ANOVA (Program 7D of BMDP-87; Dixon 1985) in the binomial format. Two data sets were identified with full cells in order to meet the requirements of the test: (1) all seasons for the years 1982–85 (called four-season-four-year data set); and (2) three seasons (spring, summer, and autumn) for 1982–86 (called three-season-five-year data set). We identified prey taxa that showed significant season, year, and season-year interaction differences in their occurrence through time using Browne-Forsythe analysis of variance for unequal variances. For the pre-El Niño, El Niño, and post-El Niño comparisons, we tested for differences in presence or absence of the same nine prey taxa using two-way Browne-Forsythe ANOVA (Dixon 1985) in the binomial format.

We also examined temporal differences in the relative number of different prey taxa found per scat (1, 2, 3, 4, 5, or >5). Pearson's chi-square test (Dixon 1985) was used to test for differences among numbers of prey occurring per scat.

Results

Identification of prey remains

In the 1476 scats collected (Table 1), we found the following: (1) 1455 scats (98.5%) contained fish remains (i.e., bones, otoliths, or eye lenses); (2) 525 scats (35.5%) contained cephalopod remains (i.e., beaks or eye lenses); (3) 1309 scats (88.6%) contained fish otoliths, cephalopod beaks, or other prey remains that were used to identify prey; (4) 1271 scats (86.1%) contained fish otoliths; and (5) 344 scats (23.3%) contained cephalopod beaks.

We identified 95.4% of 2647 prey occurrences to species, genus, or family (Table 2). Of the 2,647 prey occurrences, 75.2% were bony fishes, 14.1% were cephalopod, 10.5% were crustacea (99.3% of crustacea were pelagic red crab), and 0.2% were cartilaginous fish. We identified 44 prey taxa to species level and 8 to genus level. Seven prey taxa occurred in >10% of scats: northern anchovy *Engraulis mordax* (51.3%); jack mackerel *Trachurus symmetricus* (24.6%); pelagic red crab *Pleuroncodes planipes* (21.2%); Pacific whiting *Merluccius productus* (19.6%); rockfishes, *Sebastes* spp. (19.0%); market squid *Loligo opalescens* (16.3%); and blacksmith *Chromis punctipinnis* (10.7%). Two prey taxa occurred in 5.0–10.0% of the scats: Pacific mackerel *Scomber japonicus* (9.5%) and octopus, *Octopus* spp. (5.1%). We identified 17 species and two genera of fish, and two species and one genus of cephalopod not reported previously as prey of California sea lions (Table 2).

Nearly half of the scats (46.1%) contained only one prey taxa (Fig. 2). Northern anchovy constituted 56.2% of 603 scat samples with single prey taxa (Fig. 3).

Variability in diet through time

We found differences in distributions of occurrence (occurrence and composition indices) and numbers of individuals (number index) for nine prey taxa examined for temporal variability during the pre-El Niño, El Niño, and post-El Niño periods (Fig. 4). The distributions of occurrence were significantly different for Pacific whiting, northern anchovy, jack mackerel, Pacific mackerel, market squid, octopus and pelagic red crab ($P<0.01$). Northern anchovy occurred frequently and in the highest numbers of any prey taxa in all three periods. During the pre-El Niño period, jack mackerel occurred in the scat samples more often than the other prey; and jack mackerel and market squid were found in greater indi-

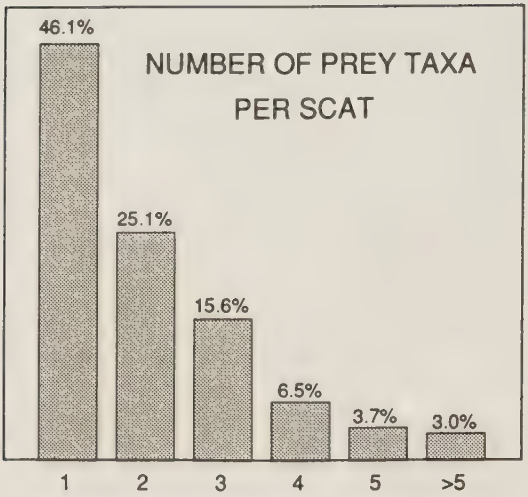


Figure 2
Occurrence of single and multiple prey taxa in 1309 California sea lion scats collected at San Clemente Island, California.

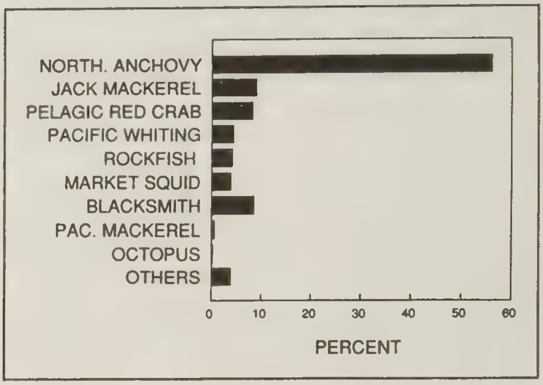
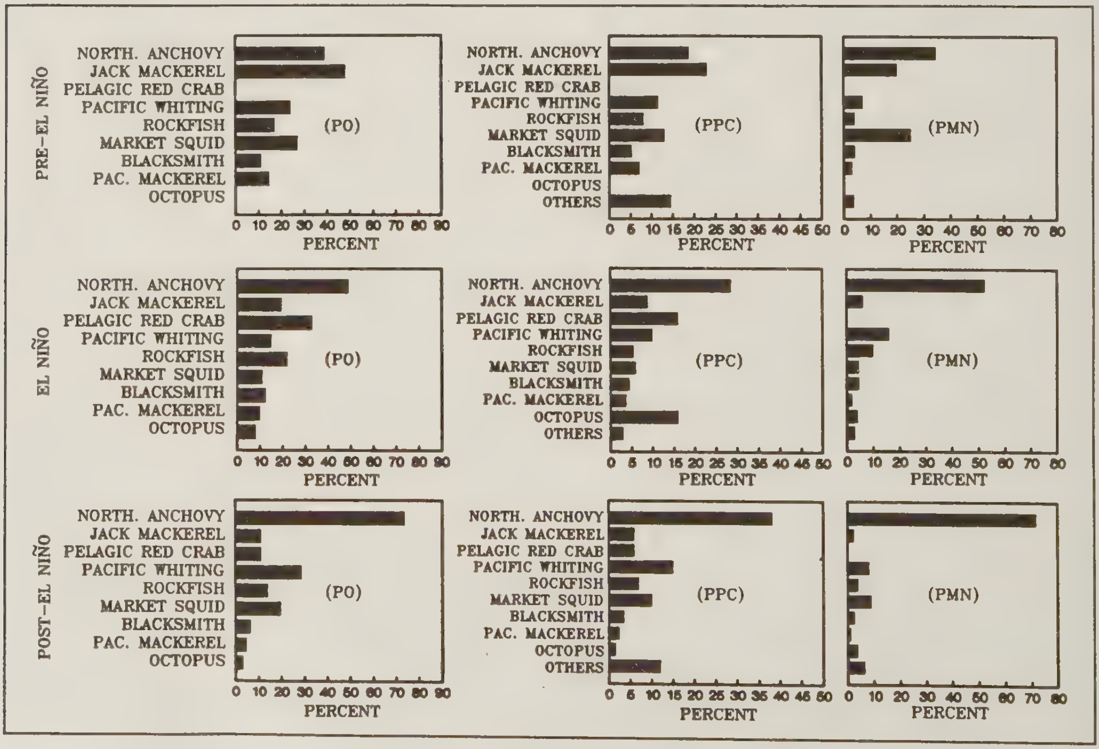


Figure 3
Percent prey found in 603 California sea lion scats with single prey taxon.

Figure 4
Occurrence (PO), composition (PPC), and number (PMN) indices of 9 prey taxa found in 1309 California sea lion scats collected at San Clemente Island, California, 1981–86, which are divided into pre-El Niño (September 1981–August 1982), El Niño (November 1982–September 1984), and post-El Niño (November 1984–September 1986) periods. The number index (PMN) could not be determined from fragments of pelagic red crab.



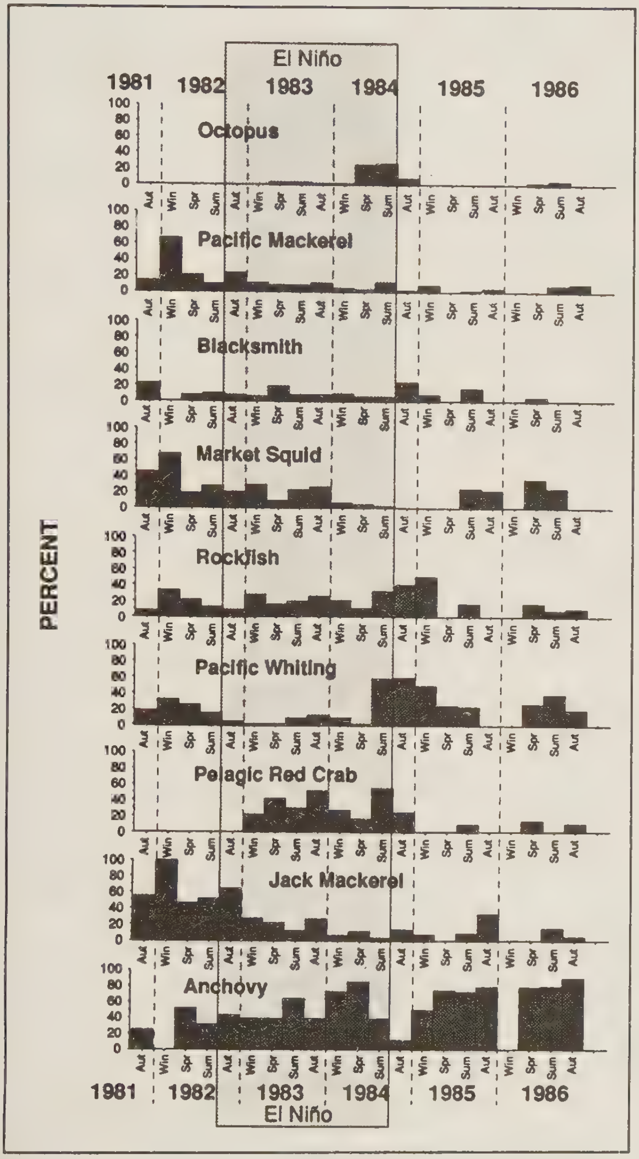


Figure 5

Seasonal percent occurrence (PO) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

vidual numbers than other prey taxa, except northern anchovy. During the El Niño period, pelagic red crab were the second most frequently occurring prey in scat samples. During the post-El Niño period, the diet was dominated by northern anchovy.

We found yearly and seasonal variability in the relative proportions represented by the three indices for 9 prey taxa examined (Figs. 5–7). Northern anchovy was consistently found in scats throughout the study at varying occurrence, composition, and number index levels. However, during summer and autumn 1984 we noted a drop in the three indices compared with 1982, 1983, 1985, and 1986; and it did not occur as often in 1982 as in 1983, 1985, and 1986. Jack mackerel was the most frequent prey during 1981–82, but after that period it was found infrequently, represented a very small proportion of the diet, and few individuals were found in the scats. An increase in the occurrence of

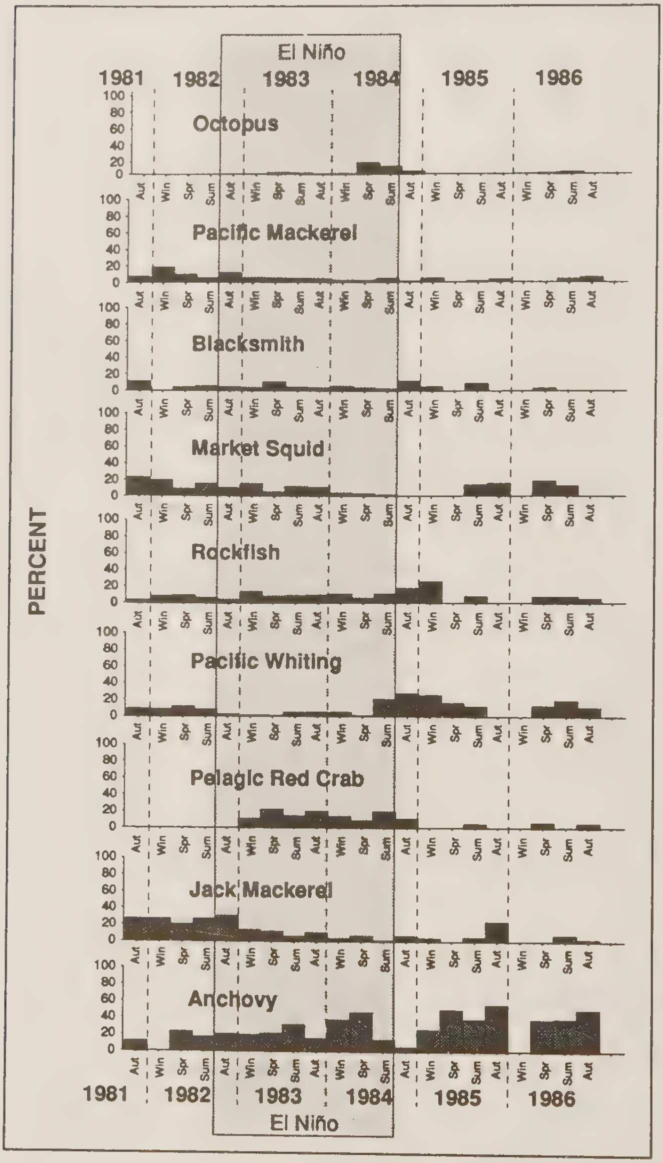


Figure 6
Seasonal percent prey composition (PPC) of 9 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

Pacific whiting was found during summer–autumn 1984 and winter 1985 when many individuals were found in scats. Rockfish was consistently found in scats throughout the study, but more individuals were represented during summer–autumn 1984 and winter 1985 than other times. Market squid was found in extremely low occurrence, composition, and number index levels (≤5.6%) or was absent from scat samples from winter 1984 through spring 1985. Pelagic red crab occurred primarily during the 1983–84 California El Niño period. Pacific mackerel occurred in the scat samples more often in 1982 than during the following years, but was represented by few individuals from 1981 to 1986. Blacksmith occurred in scat samples throughout the 1981–84 period, but during the 1985–86 period it occurred inconsistently in the diet. Octopus appeared in the samples from spring 1983 to autumn 1984, and spring–summer 1986.

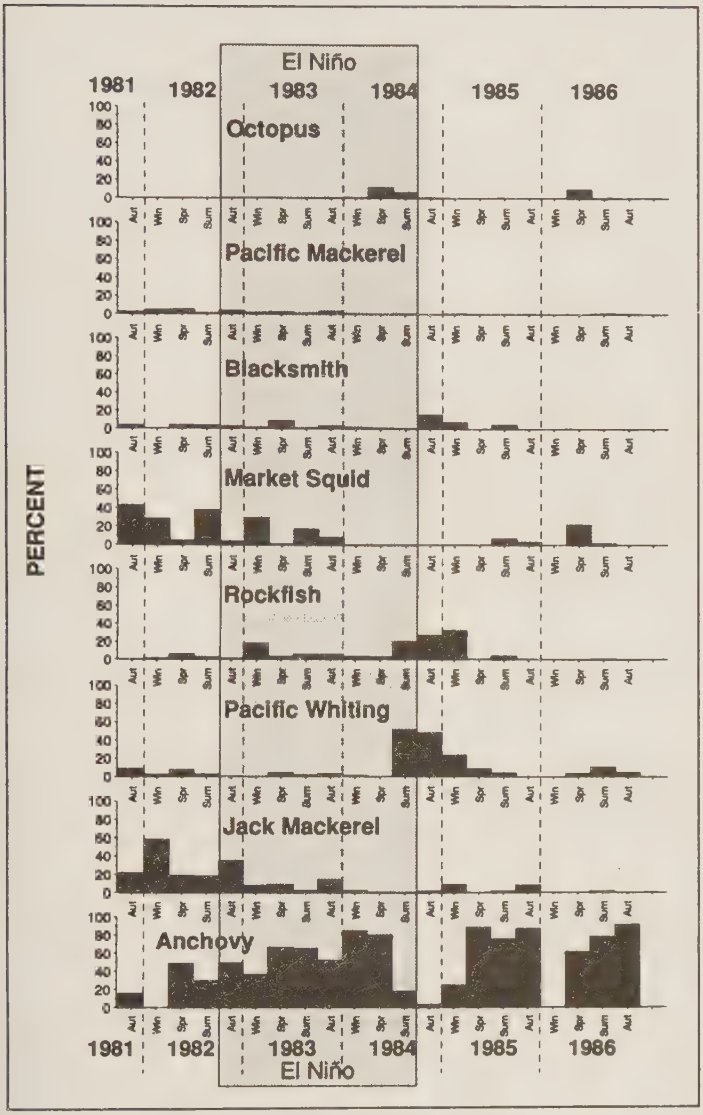


Figure 7

Seasonal percent minimum number (PMN) of 8 prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986. PMN could not be determined from fragments of pelagic red crab.

Analyses of the three-season-five-year and four-season-four-year data sets indicated significant differences ($P \leq 0.05$) in the occurrence of some, but not all, of the nine prey tested. Variances of occurrence were significantly different for all nine prey (Levene's test, $P \leq 0.05$). The three-season-five-year data set showed 21 significant differences in year, season, or season-year interactions, and the four-season-four-year data set showed 14 significant differences in year, season, or season-year interactions. Because the three-season-five-year data set included more of the post-El Niño period, results from that data set were used to interpret seasonal and yearly changes in prey items. Northern anchovy, jack mackerel, Pacific whiting, and octopus showed significant seasonal, yearly, and season-year interaction differences ($P < 0.01$). Pelagic red crab, rockfish, market squid, and blacksmith showed only significant yearly and season-year interactions differences ($P < 0.01$). Pacific mackerel had a significant difference only among years ($P < 0.01$).

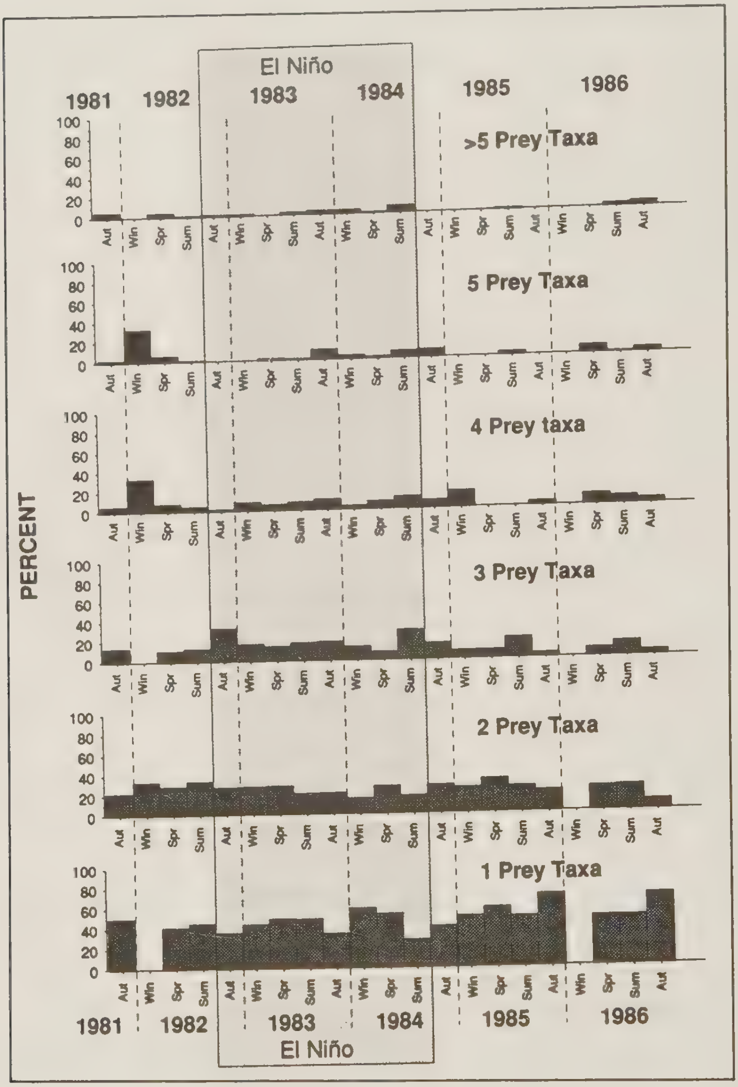


Figure 8
Seasonal occurrence of single and multiple prey taxa found in 1304 California sea lion scats, 1981–86. No samples were collected in winter 1986.

The relative frequencies of different prey taxa per scat varied among seasonal sampling periods during the study period (Fig. 8). Relative frequencies of prey taxa per scat for years 1982–85 were the same for all seasons in 1983 ($\chi^2 = 22.067$, df = 15, $P = 0.1061$) and 1985 ($\chi^2 = 18.219$, df = 15, $P = 0.2513$), but greater numbers of prey taxa were found in scats in 1982 ($\chi^2 = 35.892$, df = 15, $P = 0.0018$) and 1984 ($\chi^2 = 44.046$, df = 15, $P = 0.0001$).

Discussion

California sea lions using SCI consumed a variety of prey, consisting primarily of fish and cephalopods as indicated by the presence of fish remains in 98.5% of the scats and cephalopod remains in 35.5% of the scats. They fed on schooling fishes (e.g., northern anchovy, jack mackerel, Pacific mackerel, Pacific whiting, blacksmith, and rockfish), schooling cephalopods (e.g., market squid; Hurley 1978), and pelagic crustaceans that drift in large swarms (e.g., pelagic red crab; Boyd 1967). Our temporal analysis of nine prey taxa indicated seasonal and yearly variability in the diet of SCI sea lions. Northern anchovy apparently was the major food source because it was represented by high index values and consistently occurred in the sea lions' diet during the 5-year period. Pelagic red crab, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel appear to supplement the diet of California sea lions.

A major uncertainty with using scat analysis to study pinniped food habits is how these results reflect what was initially consumed by the animals. Studies on captive pinnipeds indicate that recovery rates are (1) lower than ingestion rates for all prey; (2) lower for prey species with small otoliths than prey with large otoliths; and (3) lower for young (i.e., small) prey than for older (i.e., large) prey of the same species (Hawes 1983, da Silva and Neilson 1985, Murie and Lavigne 1986, Dellinger and Trillmich 1988, Harvey 1989). Proportions of different prey species in scats were found to correspond to proportions of prey fed (Dellinger and Trillmich 1988). Pitcher (1980) found no difference between occurrence of fish in stomachs and feces of harbor seals *Phoca vitulina*, but cephalopods were under-represented in their feces.

The prey that occurred in 10% or more of scat samples ranged from small-sized (i.e., northern anchovy, market squid, and pelagic red crab) to prey that, when mature, could be potentially large-sized (i.e., Pacific whiting, jack mackerel, rockfish, and Pacific mackerel). Northern anchovy, being small-sized with small otoliths, would probably represent a higher proportion of the diet than indicated in scat samples. Market squid would also represent a higher proportion of the diet because beaks are often regurgitated and would be underrepresented in scats.

Results from SCI indicated differences in both prey composition and temporal variability from those described by Bailey and Ainley (1982) for sea lions at the Farallon Islands off central California. We found that several prey were consistently consumed (e.g., northern anchovy, jack mackerel, Pacific whiting, rockfish, market squid, blacksmith, and Pacific mackerel), whereas they reported only two prey (Pacific whiting and rockfish) that were regularly eaten. They found Pacific whiting to occur in the sea lions' diet during spring and summer, and juvenile rockfish during the fall and winter. At SCI we found that the presence of various types of prey in the diet of sea lions fluctuated year-to-year and sometimes seasonally within the same year. These differences between two island areas may be due to differences in the sampling periods (1981–86 for our study; 1974–78 for the Farallon Island study), to differences in prey availability in each area, or to differences in the sexual composition of animals inhabiting each area.

We would expect similar diets for sea lions using islands within close proximity of each other. Data from a study of food habits on San Miguel Island (SMI) during spring and summer in 1978–79 by Antonelis et al. (1984) were compared with our results. Four types of prey taxa (Pacific whiting, rockfish, northern anchovy, and market squid) were consistently found in scats of SCI and SMI sea lions. Jack mackerel, consistently found at SCI, was a minor prey item at SMI. The presence of pelagic red crab at SCI was due to the California El Niño, which did not occur during the SMI study. Blacksmith were not found in the diet of sea lions at San Miguel Island, but occurred frequently in the SCI study. Because the distribution and availability of these prey differ over time, we are unable to test our expected similarities in prey consumption until concurrent studies are conducted.

Availability and abundance of sea lion prey have been demonstrated by Bailey and Ainley (1982) and Antonelis et al. (1984) to influence diet of California sea lions. Evidence that abundance, if not availability, of prey influences consumption is also found from our study at SCI when we compare anchovy occurrence in scats with anchovy biomass estimates for each year (Bindman 1986, Methot and Lo 1987). The decline in the occurrence of anchovy in the scats during 1982 and 1984 coincided with lower estimates of anchovy biomass of 415,000 mt for 1982 and 309,000 mt for 1984 (Bindman 1986). Increased occurrence of anchovy in scats during 1983, 1985, and 1986 coincided with greater estimates of anchovy biomass: 623,000 and 522,000 mt (Bindman 1986), and 764,000 mt (Methot and Lo 1987), respectively. Decline in anchovy biomass may have caused SCI sea lions to consume other species in 1982 and 1984, resulting in increased occurrence in the latter.

There was more variability in occurrence of different prey taxa per scat in 1982 and 1984 when the estimated population biomass of anchovy was low, and less variability in 1983 and 1985 when there was a greater biomass. The diet of SCI sea lions, therefore, may be strongly affected by the abundance of northern anchovy. As anchovy becomes scarce, we expect SCI sea lions to consume other types of prey and exhibit greater variability in the number of different prey consumed.

We expected the non-El Niño periods to have similar occurrences of prey taxa consumed, which would differ from the El Niño distribution. In fact, all three periods exhibited significantly different distributions of prey taxa and in their occurrence.

The pattern in the commercial harvest of market squid (which is not affected by regulations and quotas) observed in California before, during, and after El Niño (Worcester 1987) closely resembled the pattern observed in the occurrence of this prey in the diet of SCI sea lions. During the El Niño in 1983 and 1984 the commercial catch of market squid was 2010 and 622 short tons, respectively; prior to the El Niño it was 25,915 and 17,951 short tons for 1981 and 1982, respectively; and, after the El Niño it was 11,326 and 23,124 short tons for 1985 and 1986, respectively. The presence of market squid in the diet of sea lions during 1983 indicates the availability of this prey to sea lions, despite low availability to commercial catches. However, in 1984 when the commercial harvest was at its lowest, market squid was not detected in the sea lions' diet. Both the sea lions' consumption of market squid and the commercial catch were apparently affected by availability.

The effect of El Niño on the diet of SCI sea lions is also demonstrated by the presence of remains from pelagic red crabs in scat samples. Pelagic red crabs are normally found over the continental shelf of southern Baja California, and are sometimes transported into the SCB and further northward by the Davidson and California Countercurrents in January and February (Boyd 1967). These currents intensified as a result of the 1982–83 El Niño/Southern Oscillation, affected water temperatures in the SCB from late 1982 to October–November 1984, and carried pelagic red crabs from southern Baja California to the SCB where they were eaten by California sea lions.

The food consumed by the U.S. population of California sea lions could have an impact on the ecosystem and be in direct competition with commercial and sport fisheries. Six of the common prey of California sea lions identified at SCI (jack mackerel, northern anchovy, market squid, Pacific mackerel, Pacific whiting, and rockfish) are of value to commercial or sport fisheries. DeMaster (1983) estimated that California sea lions in U.S. waters (estimated population size 69,700) consumed roughly 115,000–295,000 mt of biomass per year. The present consumption would be greater than in 1983 because of the estimated 5% annual increase in the U.S. population (DeMaster et al. 1982). The growth in the sea lion population, and its estimated consumption, raises questions. Will there be greater competition between sea lions and fishermen for fish and squid as a result of increased numbers of sea lions? What will be the effect of population growth of sea lions on other elements of the SCB ecosystem?

Observed temporal differences in diet of sea lions from SCI during the California El Niño of 1982–84 clearly indicate the need for long-term studies of food habits of this predator throughout its range. Short-term studies may reflect oceanographic conditions of relatively short duration, such as El Niño, that strongly influence food supply and sea lion diet.

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Citations

Antonelis, G.A., C.H. Fiscus, and R.L. DeLong
1984 Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California 1978–1979. Fish. Bull., U.S. 82:67–76.

Bailey, K.M., and D.G. Ainley
1982 The dynamics of California sea lion predation on Pacific whiting. Fish. Res. (Amst.) 1:163–176.

Bindman, A.G.
1986 The 1985 spawning biomass of the northern anchovy. Calif. Coop. Oceanic. Fish. Invest. Rep. 27:16–24.

Boyd, C.M.
1967 The benthic and pelagic habitats of the red crab, *Pleuroncodes planipes*. Pac. Sci. 21(3):394–403.

da Silva, J., and J.D. Neilson
1985 Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42:1439–1442.

Dellinger, T., and F. Trillmich
1988 Estimating diet composition from scat analysis in otariid seals (Otariidae): Is it reliable? Can. J. Zool. 66:1865–1870.

DeMaster, D.P.
1983 Annual consumption of northern elephant seals and California sea lions in the California current. Calif. Coop. Oceanic Fish. Invest. (CalCOFI) Annu. Conf. 1983, Program and Abstracts (unpaginated).

DeMaster, D.P., D.J. Miller, D. Goodman, R.L. DeLong, and B.S. Stewart
1982 Assessment of California sea lion fishery interactions. *In* Marine mammals: Conflicts with fisheries, other management problems, and research needs, p. 253–264. Trans. 47th N. Am. Wildl. Nat. Resour. Conf.

Dixon, W.J.
1985 BMDP 1987 IBM-PC program version. BMDP Statistical Software, Inc., 1440 Sepulveda Blvd., Los Angeles, CA 90025.

Eschmeyer, W.N., E.S. Herald, and H. Hammann
1983 A field guide to Pacific coast fishes of North America from the Gulf of Alaska to Baja California. Houghton Mifflin, Boston, 336 p.

Fiedler, P.C., R.D. Methot, and R.P. Hewitt
1986 Effects of California El Niño 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Fiscus, C.H., and G.A. Baines
1966 Food and feeding behavior of Steller and California sea lions. J. Mammal. 47(2):195–200.

Harvey, J.T.
1989 Assessment of errors associated with harbour seal (*Phoca vitulina*) faecal sampling. J. Zool. (Lond.) 219:101–111.

Hawes, S.D.
1983 An evaluation of California sea lion scat samples as indicators of prey importance. M.A. thesis, San Francisco State Univ., California, 50 p.

Hurley, A.C.
1978 School structure of the squid *Loligo opalescens*. Fish. Bull., U.S. 76:433–442.

Iverson, I.L.K., and L. Pinkas
1971 A pictorial guide to beaks of certain eastern Pacific cephalopods. Calif. Dep. Fish Game, Fish. Bull. 152:83–105.

McGowan, J.A.
1984 The California El Niño 1983. Oceanus 27(2):48–51.

Methot, R.D., and N.C.H. Lo
1987 Spawning biomass of the northern anchovy in 1987. SWFC Admin. Rep. LJ-87-14, Southwest Fish. Cent., Natl. Mar. Fish. Serv., P.O. Box 271, La Jolla, CA 92038-0271, 46 p.

Murie, D.J., and D.M. Lavigne
1986 Interpretation of otoliths in stomach content analysis of phocid seals: Quantifying fish consumption. Can. J. Zool. 64:1152–1157.

Oliver, C.W., and M.S. Lowry
1987 Pinniped studies conducted between August, 1981 and December 1982 at San Clemente Island, California. SWFC Admin. Rep. LJ-87-23, Southwest Fish. Cent., Natl. Mar. Fish. Serv., P.O. Box 271, La Jolla, CA 92038-0271, 47 p.

Pitcher, K.W.
1980 Stomach contents and feces as indicators of harbor seal, *Phoca vitulina*, foods in the Gulf of Alaska. Fish. Bull., U.S. 78:797–798.

Scheffer, V.B., and J.A. Neff
1948 Food of California sea lions. J. Mammal. 29(10):67–68.

Stewart, B.S., and P.K. Yochem
1984 Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. Bull. South. Calif. Acad. Sci. 83(3): 121–132.

Worcester, K.
1987 Market squid. *In* Review of some California fisheries for 1986 (compiled by J. Grant). Calif. Coop. Oceanic Fish. Invest. Rep. 28:11–20.

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The Flow of the Undercurrent Over the Continental Borderland off Southern California

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Complex bathymetric features offshore of southern California have a pronounced effect upon the flow of the California Undercurrent. Geostrophic dynamics and water mass characteristics are used to reveal the various paths of flow and spread of undercurrent waters for a July 1985 survey. Undercurrent waters are identified by relatively high spiciness and low dissolved oxygen at densities between $\sigma_t = 26.4$ and 26.9 (~200 to 400 m). A jetlike core of flow follows the continental slope within the California Bight and exits the bight through a gap in the Santa Rosa–Cortes Ridge. Mixtures that include undercurrent waters exit the bight through other gaps in the bathymetric ridge and about the southern end of the ridge. As evidenced by patterns in the fields of geostrophic currents and water mass characteristics, baroclinic instabilities develop about the ridge which result in the diversion of undercurrent waters offshore beneath the California Current and into the offshore mesoscale eddy field. The offshore subsurface diversion of undercurrent waters and their inclusion in the offshore mesoscale eddy field are also found in the long-term mean distributions for July.

1. INTRODUCTION

The bottom topography off southern California has been termed a continental borderland to distinguish it from the ordinary shelf-slope morphology found along most continental margins [*Shepard and Emery*, 1941]. Islands, shallow banks, basins, and troughs form a complex bathymetric region extending from the coast to 200 km offshore. The southern California coastline has a concave curvature between the headland at Point Conception to the U.S.–Mexican border. As a whole, this region is referred to as the California Bight. The geographic–bathymetric configuration of the bight exerts a pronounced influence upon the local circulation patterns and hence upon the distributions of physical [e.g., *Sverdrup and Fleming*, 1941] and biological quantities [e.g., *Allen*, 1945; *Owen*, 1980]. During 1985 we conducted an oceanographic survey off southern California. The sampling grid was designed to reveal the influence of the geographic–bathymetric features upon the circulation of the California Current system (CCS), especially the flow of the California Undercurrent (CU). The survey grid also includes station lines across the core of the California Current (CC) and transects an offshore dipole eddy [*Simpson and Lynn*, this issue]. The station grid of this study differs considerably from that used by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys in both its spatial resolution and depth of sampling. The objectives of this report are (1) to examine the spatial continuity of the CU through the complex bathymetry of the bight, (2) to trace the poleward paths and offshore spread of waters of southern origin transported by the CU, (3) to contrast this subsurface flow with the surface flow, and (4) to compare these results with the long-term CalCOFI mean conditions.

2. BACKGROUND

The CC, a slow, broad equatorward flow, is the eastern limb of the large-scale anticyclonic gyre of the temperate North Pacific Ocean. The CC carries relatively cool, low-salinity waters of subarctic origin to lower latitudes. On average, the core of the CC has velocities of 0.10 to 0.15 m s^{-1} and traces a path roughly parallel to the California–Baja California coastline. Localized measurements of flow can exceed 0.5 m s^{-1} [*Davis*, 1985]. An instantaneous realization of the CC includes a tangle of meanders, eddies, and narrow jetlike flows and counterflows. The CC lies at varying distances off the coast, and at the latitude of the U.S.–Mexican border there is a strong shoreward component to the flow. In most seasons (especially summer) the flow splits; one branch turns and flows northward into the California Bight, becoming the eastern limb of a cyclonic eddy centered about the offshore banks. Seasonally (fall and winter) a weak Inshore Countercurrent (IC) develops at the surface along various portions of the coastline [*Reid et al.*, 1958]. At depth the CU carries waters of subtropical origin poleward along the continental slope. These waters are relatively warm and saline and have low concentrations of dissolved oxygen. The CU also demonstrates a well-defined seasonality and at times opposes the overlying surface flow. Maps and sections of the long-term seasonal means of relative geostrophic velocity and distributions of ocean characteristics for the CCS are available in CalCOFI Atlas 30 [*Lynn et al.*, 1982]. For a comprehensive review of the long-term seasonal, large-scale description of the CCS, the reader is referred to recent papers by *Hickey* [1979], *Chelton* [1984], and *Lynn and Simpson* [1987] and to important references of pioneering work given therein.

The waters of the bight were first studied in detail by *Sverdrup and Fleming* [1941], who presented a very perceptive study based on a series of three cruises conducted in the spring and summer of 1937. They identified a shallow poleward flow (that they termed the Southern California Counter Current) as part of a large cyclonic eddy. They recognized that this current is different from a deep poleward current (the CU) which carries characteristically

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different water. They suggested that the topography of the bottom plays a large part in determining the character of the currents, especially the subsurface currents. In an examination of the different water masses, they identified waters of northern and southern origins and showed that part of the southern water flows through the deeper gaps in the submerged ridge that projects south-southeast from Santa Rosa Island. From there the flow continues north. They also argued that large-scale mixing must take place between the CC and the countercurrents. They hypothesized that the mixing is brought about by eddies because their data showed that patches of water, of mostly southern origin, were surrounded by water of mostly northern origin.

Direct measurements of the CU off central California were made by *Reid* [1962] using drifters tethered to drogues at 250 m. He found speeds of 0.23 m s^{-1} within 74 km of the coast. Using a profiling current meter, *Wooster and Jones* [1970] showed that the CU off Punta Colnett, northern Baja California, can manifest itself as a narrow (20 km) ribbon of flow having an average speed of 0.3 m s^{-1}. The seasonal variation of the geostrophic velocity and associated characteristics of temperature, salinity, and dissolved oxygen at levels of the CU were described for the cardinal CalCOFI station lines, from central California to southern Baja California, by *Lynn and Simpson* [1987]. CalCOFI line 90 bisects the California Bight and provides the long-term seasonal means for this study. The extensive CalCOFI data are most useful for examining mesoscale to large-scale processes but lacks the spatial resolution necessary to examine bathymetric interactions with the flow of the CU in the bight, especially its continuity and path.

3. THE OBSERVATIONS

The station positions for the RV *David Starr Jordan* survey of July 11–27, 1985, are given in Figure 1. Principal landmarks are identified in the caption. Within the California Bight, station lines are perpendicular to the local continental slope; they cross channels and basins between islands, banks, and the mainland. West and southwest of the bight the station lines lie perpendicular to the path of the CC as given by the long-term July mean pattern of dynamic height [*Lynn and Simpson*, 1987]. The double cross of stations west of 122°W overlays an eddy dipole observed in satellite surface temperature patterns for July 9, 1985 [*Simpson and Lynn*, this issue]. Most of the spacing between stations varies between 12 and 22 km; it is less than 12 km where it was necessary to accommodate narrow channels. Where bottom depth permitted, conductivity-temperature-depth-oxygen (CTDO2) (Neil Brown Inc. Mark III) casts were made to 1000 m (1200 m in the eddy dipole). Within the bight, where bottom depth is mostly less than 1000 m, station transects begin and end at the 500-m isobath. All eight stations in the Santa Barbara Channel are less than 500 m, as are several stations near the outer banks.

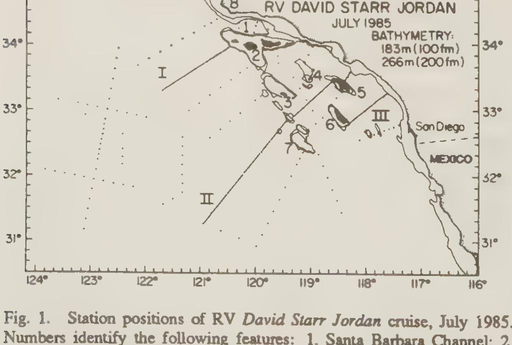

Fig. 1. Station positions of RV *David Starr Jordan* cruise, July 1985. Numbers identify the following features: 1, Santa Barbara Channel; 2, Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa); 3, San Nicolas Island; 4, Santa Barbara Island; 5, Santa Catalina Island; 6, San Clemente Island; 7, Tanner and Cortes banks; and 8, Pt. Conception. Roman numerals identify station lines used in subsequent figures.

Beam transmission was measured at 660 nm using a beam transmissometer with a 25-cm path length (Sea Tech, Inc.) attached to the CTD. Beam transmission is a good indicator of concentration of suspended matter and is used to differentiate near coastal water, having suspensoids of plankton and terrigenous materials, from the more sterile oceanic waters. A 12-bottle rosette was used to obtain temperature, salinity, and oxygen calibration measurements for the CTDO2. Dissolved oxygen titration check samples were taken every fourth station or so, 43 stations in all. Twelve samples per cast were taken on 13 stations, and four or five samples were taken on the remaining 30 stations. Oxygen probe measurements were processed using an experimental algorithm developed with the assistance of the Physical and Chemical Oceanographic Data Facility at Scripps Institution of Oceanography (SIO). A single set of coefficients was applied to all casts that reduced the standard deviation between check samples and probe data to less than ±0.1 mL L^{-1}. Long-term experience has shown us that considerable problems can arise in the use of this style oxygen probe. This particular data set, on the whole, lacked serious problems and its application and interpretation herein is based on values of oxygen concentration and its gradients that greatly exceed any reasonable estimate of measurement or calibration error.

4. BATHYMETRY AND ITS EFFECT ON THE CALCULATION OF DYNAMIC HEIGHT

The Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) form an east-west ridge that, at intermediate levels, divides the Santa Barbara Channel from the remainder of the California Bight (Figure 1). The western boundary of the bight is formed by a submerged ridge projecting equatorward from Santa Rosa Island and including San Nicolas Island and Cortes and Tanner banks. This latter ridge, referred to as the Santa Rosa–Cortes (SR-C) Ridge [*Sverdrup and Fleming*, 1941] is perforated by gaps of various depths. To some degree these bathymetric features act as an impediment to the poleward-flowing CU.

It is desirable to use the greatest reference pressure available for the representation of dynamic height on the assumption that the relief in the pressure field at the deepest level is insignificant (i.e., that the absolute geostrophic velocities at this level are negligible for all practical purposes). It has long been held that a choice of 500 to 1000 dbar (1 dbar = 10^4 Pa) is sufficient for estimating the flow of shallow currents in the eastern North Pacific. A reference pressure of 1000 dbar (actually 1000 m, or approximately 1009 dbar) is available for stations west of the vicinity of the SR-C Ridge. Within the bight, however, the bottom depth is considerably less than 1000 m. There, 500 dbar has been chosen as a reference pressure. We present one set of maps of dynamic height using 500 dbar as a reference pressure and a second set using 1000 dbar, each to be applied in the appropriate region. Where a comparison can be made, the differences between the two are examined.

In three instances where an intermediate station in a line failed to reach 1000 m, we have used interpolation to fill in the missing values. We have also applied the method of extrapolating the slope of deep isopleths of dynamic height [*Montgomery*, 1941; *Reid and Mantyla*, 1976] where the depth at the station at the end of a station line does not reach 1000 m. These extrapolations are confined to stations that fall upon the slopes of the SR-C Ridge. There are not enough stations that reach 1000 m within the bight to apply the method of extrapolation to those stations that fall along the coast. The results of this extrapolation of dynamic height are entirely consistent with the larger patterns.

5. RESULTS

5.1. *Patterns of Surface Circulation*

The pattern of flow, as given by the dynamic height of the sea surface relative to 500 dbar (Figure 2*a*), shows that the core of the CC lies 90 to 170 km off Point Conception. Between 31°N and 32°N the flow turns shoreward. The cyclonic flow about the outer banks is the Southern California Eddy (SCE). Its center encircles San Nicolas Island. The flow in the coastal zone is weakly equatorward. The major features of the distribution of salinity at the shallow salinity minimum reflect the pattern of surface flow (Figure 2*b*). In general, the minimum in salinity is found at the sea surface north of Point Conception. South of Point Conception, saline surface waters of both the central eastern North Pacific and the upwelled coastal waters mix with and override the low-salinity core of the CC to form a shallow subsurface minimum in the upper thermocline [*Reid et al.*, 1958, 1964]. Except for a single station in the northwest corner of our station grid, the salinity minimum in the CC is subsurface (20 to 75 m) (Figure 2*b*). The shoreward sweep of the CC and the inshore limb of the SCE bring the shallow subsurface salinity minimum into the California Bight. Upwelling in the center of the cyclonic SCE brings the minimum to the sea surface north and east of San Nicolas Island (indicated by asterisks in Figure 2*b*). Thus upwelling within the SCE was stronger than along the coastal margin during the observational period.

Beam transmission provides an independent tracer of flow. Figure 2*c* shows the depth integral of the beam attenuation coefficient for the upper 100 m. There is a very narrow tongue of relatively turbid water having values of integrated beam coefficient in excess of 12 lying immediately seaward of the SR-C Ridge (Figure 2*c*). In contrast to these turbid waters, the CC carries a broad tongue of relatively clear oceanic waters (values less than 8) which sweeps shoreward and penetrates into the middle of the bight.

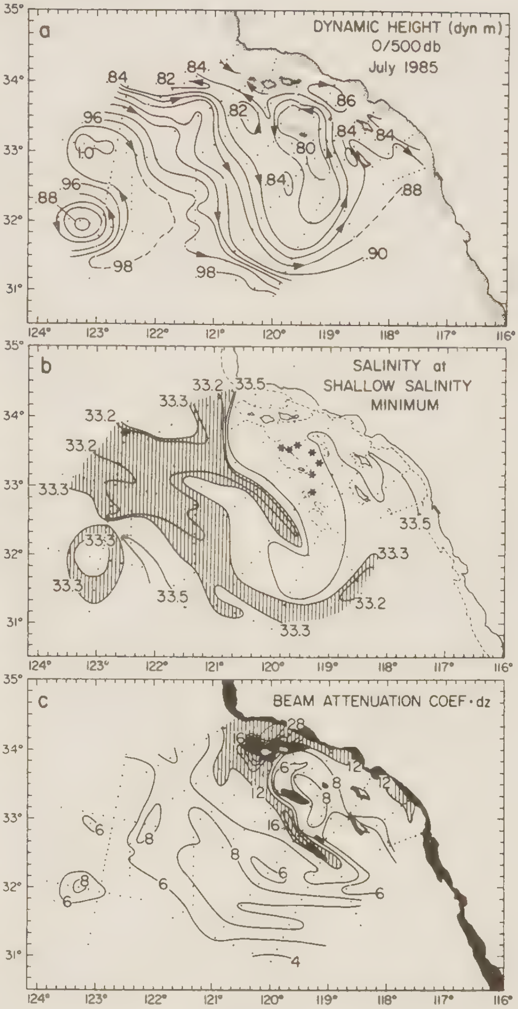

Fig. 2. (*a*) Dynamic height (dynamic meters, or $10\,m^2\,s^{-2}$) of the sea surface relative to 500 dbar. The bathymetry in this and subsequent figures of dynamic height is shown stippled. (*b*) Distribution of salinity at the shallow salinity minimum. The depth of this feature was generally less than 70 m. At eight stations (shown by asterisks) the minimum occurred at the surface. (*c*) Beam attenuation coefficient (units of reciprocal meters) integrated over the upper 100 m of the water column. Bathymetry in this and subsequent figures of distributions is shaded black.

5.2. *Patterns of Subsurface Circulation*

The most energetic flow, indicated by closely-spaced contours of dynamic height at 250 m relative to 500 dbar (Figure3*a*), occurs where the poleward-flowing CU hugs the continental slope. The main flow of the CU appears to exit the bight through the gap in the bathymetry between Santa Rosa Island and San Nicolas Island. The data also imply that part of the CC at this level turns into the bight, swings poleward, and exits the bight through a gap south of San Nicolas Island where it then joins the CU. The distributions of salinity and dissolved oxygen on the surface where $\sigma_t = 26.6$ (Figures 3*b* and 3*c*) show that the waters having the highest salinities (shaded for values above 34.2) and the lowest oxygens (shaded for values below $1.4\,mL\,L^{-1}$) are found along the path of the CU. These waters also are found within the gap north of San Nicolas Island and extend northwest from there along the continental slope of the west end of the Channel Islands. Within most of the domain of the CU this σ_t surface lies between 260 and 300 m. Waters of nearly the same characteristics are found in the Santa Barbara Channel (Figure 3). The sill depth of the eastern end (230 m) precludes significant flow at this density. Some small flow, however, may occur up and over the sill.

5.3. *Controlling Bathymetry*

Silhouettes of the controlling bathymetry (Figure 4) show that the sill depths in the gaps in the SR-C Ridge range between 362 and 480 m (excluding the shallow dip between the Cortes and

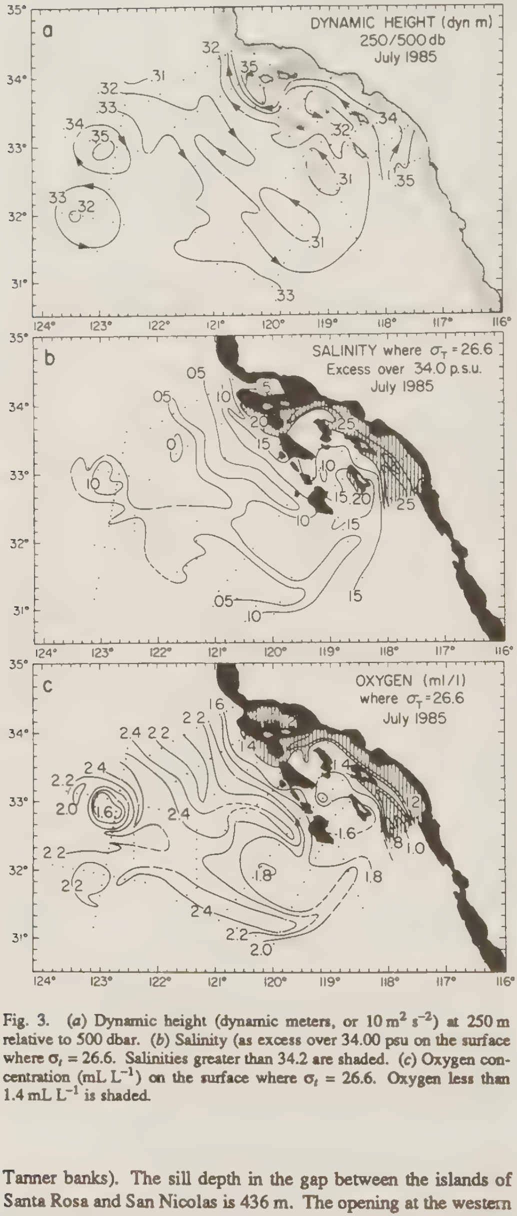

Fig. 3. (*a*) Dynamic height (dynamic meters, or $10\,\mathrm{m}^2\,\mathrm{s}^{-2}$) at 250 m relative to 500 dbar. (*b*) Salinity (as excess over 34.00 psu on the surface where $\sigma_t = 26.6$. Salinities greater than 34.2 are shaded. (*c*) Oxygen concentration ($\mathrm{mL\,L^{-1}}$) on the surface where $\sigma_t = 26.6$. Oxygen less than $1.4\,\mathrm{mL\,L^{-1}}$ is shaded.

Tanner banks). The sill depth in the gap between the islands of Santa Rosa and San Nicolas is 436 m. The opening at the western end of Santa Barbara Channel is deep (474 m) and broad, while at the eastern end it is relatively shallow (230 m) and more restricted.

5.4. *Velocity Sections*

The vertical sections of relative geostrophic velocity (Figure 5; locations shown in Figure 1) in the regions west of the SR-C Ridge exhibit bands of poleward and equatorward flow. The vertical maxima in equatorward flow (0.16 to 0.24 m s^{-1}) occur at the surface. Except for flow associated with the SCE, poleward maxima (0.06 to 0.18 m s^{-1}) occur at depths of 65 to 550 m. Within the bight the relative geostrophic velocity is almost totally poleward (Figure 5, section II). There are two maxima; the one at the surface (0.18–0.24 m s^{-1}) is the eastern limb of the SCE, and the other at 65 m (0.28 m s^{-1}) lies above the continental slope within the San Pedro Channel (between Santa Catalina Island and the mainland). The two pairs of stations that adjoin both sides of Santa Catalina have a deep poleward velocity maximum, between 200 and 240 m. The deep penetration of vertical shear evident in the San Pedro Channel suggests that there may be appreciable slope to the pressure field at 500 dbar. Hence the velocity of the CU may be underestimated there.

5.5. *Dynamic Height Relative to 1000 dbar*

The dynamic height of the sea surface relative to 1000 dbar [see *Simpson and Lynn*, this issue, Figure 9*a*] has some differences from the version using a 500-dbar reference (Figure 2*a*). Greater differences, however, are more evident at the 250-m level (Figures 3*a* and 6). Overall, there is greater topographic relief when using the greater reference pressure. The enhanced gradients in dynamic height (relative to 1000 dbar) off San Diego and south of Santa Cruz Island reveal that the CU is stronger than that indicated by using the 500-dbar reference pressure. At 250 m over 1000 dbar the CC is not a continuous flow. At this depth, most of the equatorward flowing waters appear to turn about and join the poleward flow. The SCE is not found at this level. In its place there is westward flow through gaps in the SR-C Ridge. There is a strong cyclonic eddy (marked with an E in Figure 6) centered at 31°35′N, 119°40′W which differs markedly from the surface pattern. This deep eddy has an elongated east-west configuration.

5.6. *Water Mass Characteristics*

Vertical sections of characteristics are dominated by the usual strong vertical gradients. An effective method to examine isopycnal distributions of water mass characteristics is to remove these strong diapycnal trends. This is done by calculating the anomalous differences between characteristic curves (T versus S, O_2 versus σ_t) for station data and specified mean characteristic curves. The resulting anomalies can be plotted as vertical sections and maps to reveal the distributions of the different water masses. We have chosen to create mean characteristic curves for the core region of the CC as a basis for calculating the anomalies. This choice causes the largest anomalies in this data set to occur in the CU. Figure 7 shows the location of 39 stations that were selected as most representative of the local CC for creating the mean curves. The stations selected fell within the broad southeastward flow of the CC as seen in the pattern of dynamic height (Figure 2*a*). This selection excludes stations in the SCE and eddy E because they entrain coastal waters. Also excluded were stations in the northwest and within and about the eddy dipole because of strong interleaving and entrainment of differing water types. The cast data and calculated parameters for the 39 stations were interpolated and averaged at intervals of 0.01 in σ_t. The resulting curves (heavy lines in Figures 8*a* and 8*b*) are smooth with very shallow inflections. The envelope of the variation of the 39 stations (depicted by shading) is narrow, indicating that we have identified a local water mass. The characteristic curves for station 19, located in the San Pedro Channel (Figure 7), are also shown in Figures 8*a* and 8*b* (light lines) for comparison. This station is representative of near-coastal waters. Waters at station 19 are warmer and more saline than the 39-station average for any given density. Lines of constant σ_t (labeled 23 through 27) are

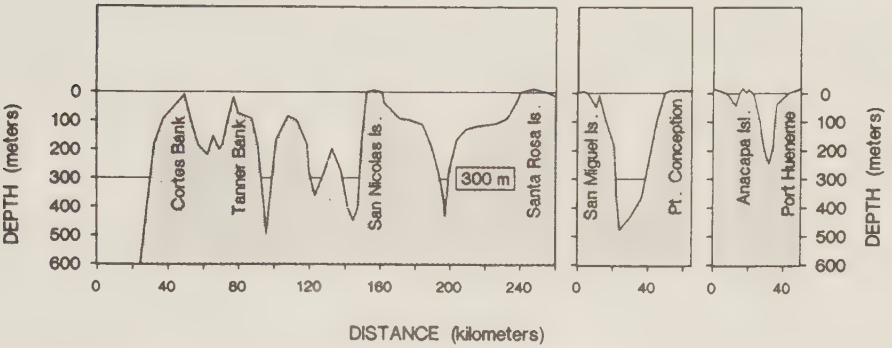

Fig. 4. Silhouettes of bathymetry showing the controlling sill depths along the Santa Rosa–Cortes (SR-C) Ridge and both ends of the Santa Barbara Channel.

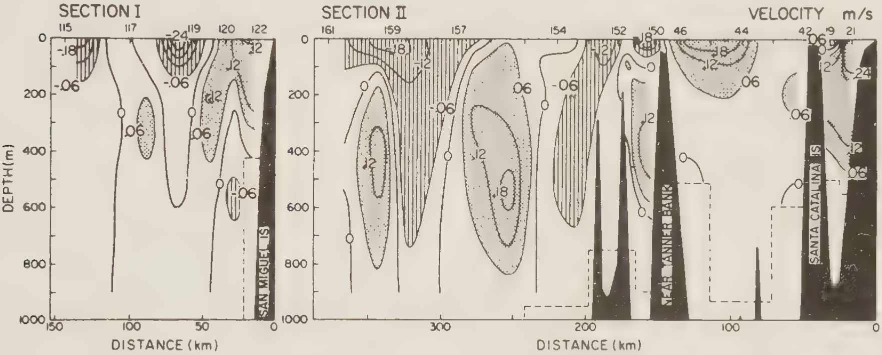

Fig. 5. Vertical sections of relative geostrophic velocity (in m s^{-1}). Locations of sections are given in Figure 1 (Roman numerals). Velocities greater than 0.06 m s^{-1} are hatched (equatorward) and stippled (poleward).

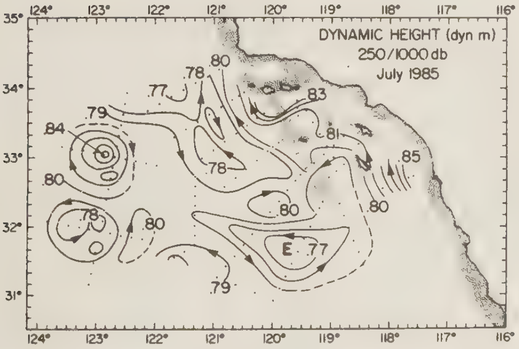

Fig. 6. Dynamic height (dynamic meters, or 10 m^2 s^{-2}) at 250 m relative to 1000 dbar. E denotes the center of a subsurface eddy.

given in Figure 8*a*. The set of lines that are nearly orthogonal to σ_t represents constant values of spiciness (labeled -1 through 3). Spiciness (symbol π), a function of temperature and salinity, was formulated to scale temperature–salinity differences along lines of constant σ_t [*Stommel*, 1962; *Munk*, 1981]. We calculate spiciness by the method of P. Flament (A note on seawater spiciness and diffusive stability, submitted to *Deep-Sea Research*, 1989). A concise mathematical definition of spiciness based upon Flament's derivation is given by *Simpson and Lynn* [this issue]. We use it as a tracer to measure the deviation of water characteristics from a mean *T–S* curve. In this context, waters having a positive anomaly of spiciness are both warmer and more saline than the chosen standard; and vice versa. The deviation or anomaly of station 19 from the mean *T–S* curve at a level where σ_t = 26.6 is shown in Figure 8*a*. This anomaly shows the difference between CC and CU waters (σ_t = 26.6 occurs at 260 m for station 19). At densities less than σ_t = 25.6, station 19 has higher values of dissolved oxygen than the 39-station mean; at greater densities it is the reverse (Figure 8*b*). CU waters at σ_t = 26.6 have an oxygen anomaly of approximately -1 mL L^{-1}.

Although station 19 is more spicy than the 39-station mean at any given density (Figure 8*a*), it has layers that are both more and less spicy as a function of depth (Figure 8*c*). This difference is a consequence of the overall upward tilt toward shore of the density field in response to large-scale dynamics. If anomalies are computed using depth as the ordinate, the result combines the effects of both the geostrophic (vertical) displacement of the density field and the water mass differences seen in *T–S* diagrams.

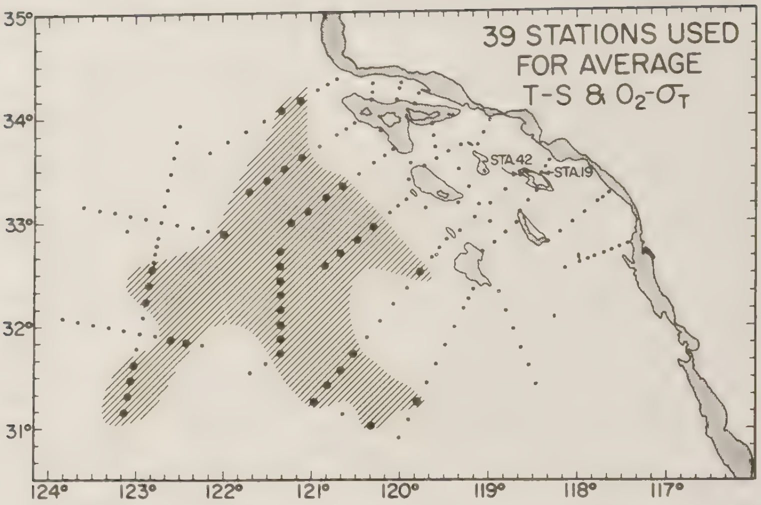
39 STATIONS USED
FOR AVERAGE
T-S & O2-σT
STA.42
STA.19
35°
34°
33°
32°
31°
124°
123°
122°
121°
120°
119°
118°
117°

Fig. 7. Location of 39 stations used to create mean T–S and O_2–σ_t curves.

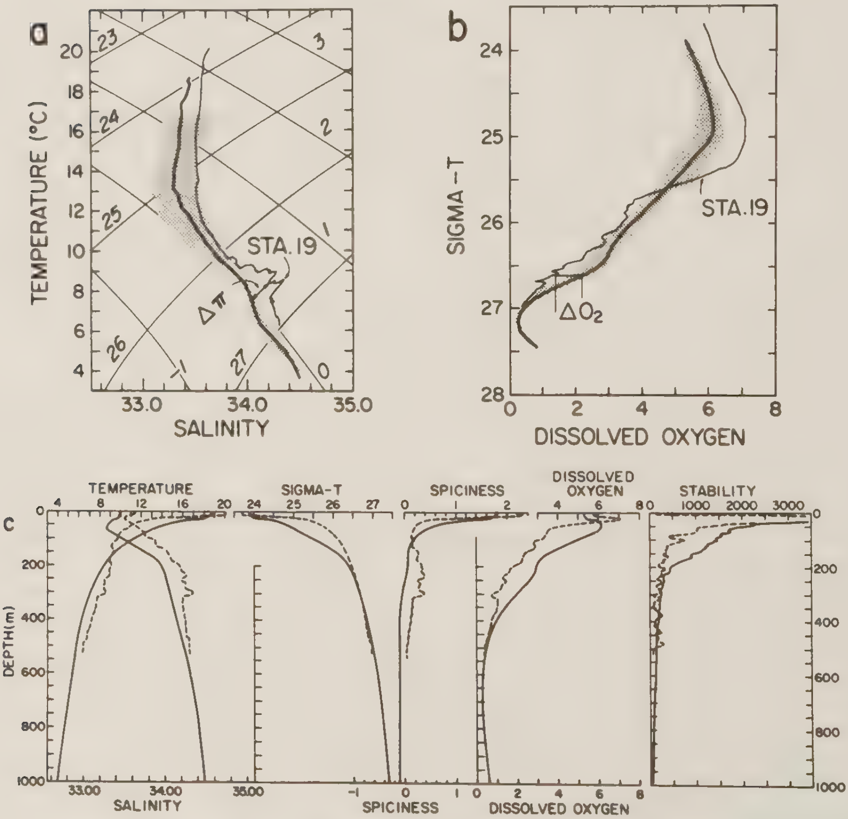

Fig. 8. (a) Temperature–salinity diagram with lines of σ_t (labeled 23 to 27) and spiciness (labeled -1 to 3). The average curve for the 39 stations of Figure 7 is given by the heavy line, and the range is shown by shading. Station 19 is given by the thin line. The difference in spiciness ($\Delta\pi$) between these curves at σ_t = 26.6 is shown. (b) The same as Figure 8a, except for σ_t versus oxygen. (c) Vertical profiles of characteristics for the 39-station averages (solid lines) and for station 19 (dashed lines). All averaging (including depth) was done at common levels of σ_t. Hydrostatic stability has units of $m^{-1} \times 10^8$.

5.7. *Vertical Sections of Anomalies*

The largest anomalies of spiciness (>3) and dissolved oxygen (<-9) occur in the southern part of the bight in layers at intermediate depths (section III, Figure 9; location of sections given in Figure 1). These and all other anomalies reported herein are multiplied by 10. Without further specification, dissolved oxygen anomaly is given as × 10 mL L^{-1}, and spiciness anomaly is given in × 10 units of σ_t. Peak values of positive spiciness anomaly occur near 350 m, and those of negative oxygen anomaly occur near 230 m. These subsurface layers of extremes are also found outside of the SR-C Ridge, off San Miguel Island (section I, Figure 9) where their extreme values (at reduced levels) are confined within 60 km of the continental slope. Section II of Figure 9 offers a broader perspective of the distribution of anomalies. It transects the entire bight near midpoint and also most of the CC and is approximately coincident with CalCOFI line 90. Layers of subsurface anomaly extrema (positive spiciness and negative dissolved oxygen) occur throughout the bight and beyond, with the most extreme values found over the continental slope (in the San Pedro Channel). In this figure anomalous values (1 in spiciness and -3 in oxygen) extend over 280 km from shore (to station 157). In the surface domain (<75 m) the spiciness is particularly high, commensurate with the higher values of temperature and salinity caused by surface warming and evaporation and/or mixing. The shallow waters also have greater dissolved oxygen because of local biological and physical processes. Between the shallow and deep maxima in spiciness in the bight there is a minimum layer

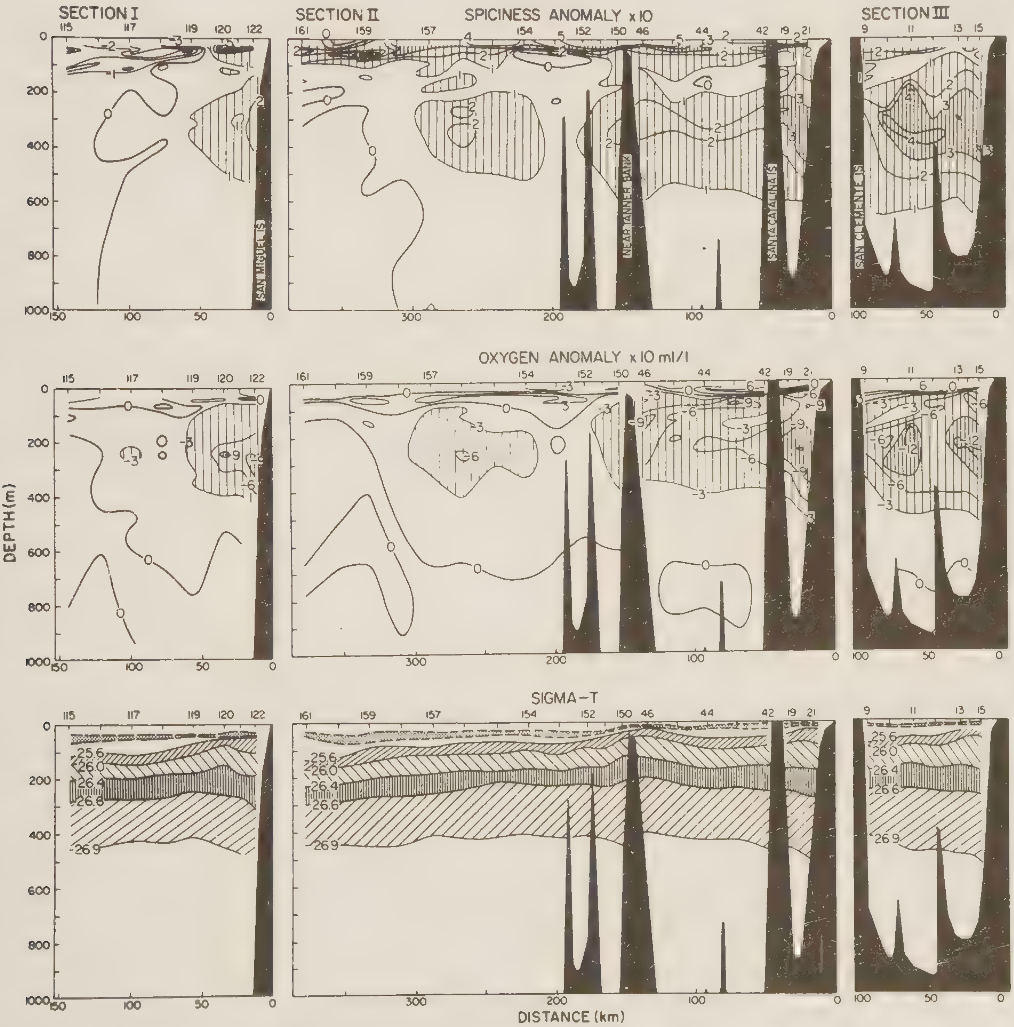

Fig. 9. Vertical sections (lines I, II and III of Figure 1) of spiciness anomaly × 10 units of σ_t, oxygen anomaly × 10 mL L^{-1}, and σ_t. Anomalies of spiciness above 1.0 and of oxygen below -3.0 are hatched. The shallow shaded layer in σ_t is the strong summer pycnocline. The four layers in σ_t that are identified in the text are indicated by differing manners of hatching.

which is more indicative of offshore waters. The oxygen anomaly pattern associated with the spiciness minimum layer differs from that of spiciness; the complex biological processes active there override the influence of transport and lateral mixing.

5.8. *Maps of Anomalies*

Four density layers, σ_t = 25.6 to 26.0, 26.0 to 26.4, 26.4 to 26.6, and 26.6 to 26.9, were selected for mapping the distribution of anomalies. Average anomaly values within these layers, rather than values at a specified σ_t surface, were used to avoid variations associated with small-scale processes that cannot be resolved by the given station spacing. These layers are centered about depths of 80, 140, 200, and 350 m, respectively (Figure 9*c*) and hereinafter are referred to as layers 1 through 4. Layer 1 lies close enough to the surface that its characteristics are affected by diapycnal mixing as well as by lateral mixing and transport, whereas in the deeper layers lateral mixing and transport are the dominant processes. The anomalies of spiciness and dissolved oxygen for layers 1 through 3 are given in Figures 10 through 12. Layer 4 is discussed but not shown. A map of acceleration potential [*Montgomery*, 1937; *Montgomery and Stroup*, 1962] for the σ_t surface found at depths that are intermediate within layer 1 is also presented (Figure 10*a*). Maps of acceleration potential (in units of dynamic meters, or 10 $m^2 s^{-2}$) provide the patterns of geostrophic flow for surfaces of variable depth.

5.8.1. *Layer 1 (σ_t = 25.6 to 26.0).* The pattern of geostrophic flow on the surface where σ_t = 25.8 relative to 1000 dbar (Figure 10*a*) differs appreciably from that found at the sea surface relative to 500 dbar (Figure 2*a*). This density surface (midway in the depth range of layer 1) is found near 50-m depth both inshore and in the SCE, and near 100- to 150-m depth offshore. From the sea surface to this density surface there is an overall decrease in geostrophic flow within the CC proper. The center of the SCE has shifted southward from San Nicolas Island to the Tanner and Cortes banks. Eddy E appears as a separate cyclonic eddy southwest of the SR-C Ridge.

Within layer 1, relatively spicy (warm and saline) waters are found along the coast and within eddy E (Figure 10*b*). The most extreme values of positive spiciness, >2, occur within the SCE and about the SR-C Ridge. The pattern within eddy E shows relatively spicy waters projecting westward from the southern end of the SR-C Ridge. Waters of relatively low spiciness penetrate from the northwest in the core of the CC. The CC waters also have relatively high dissolved oxygen in layer 1 while the waters in the bight exhibit low oxygen. The distribution of oxygen anomaly, however, shows only a very weak correspondence to that of the spiciness anomaly.

5.8.2. *Layer 2 (σ_t = 26.0 to 26.4).* The middepth of layer 2 (Figure 11) lies between 100 and 175 m. In layer 2 the spiciest and least oxygenated waters occur along the coast, penetrating northward from south of the international border. At slightly lesser values of the anomalies, spicy, low-oxygen waters lie along and on both sides of the SR-C Ridge and project westward from the southern extent of the ridge. The zero contour of spiciness anomaly forms a mushroom-shaped pattern which extends into the eddy dipole system [*Simpson and Lynn*, this issue]. The oxygen anomaly shows a similar symmetrical pattern. Waters having low values of anomalies penetrate the central bight from the southwest. The distributions of spiciness and oxygen are very similar.

5.8.3. *Layer 3 (σ_t = 26.4 to 26.6).* The middepth of layer 3 (Figure 12) lies between 200 and 260 m. Overall, the distributions of anomalies are similar to those of the layer 2, above. The range of anomalies in layer 3, however, is much greater. The maximum spiciness is 4, where it had been 2 in layer 2. The waters that exceed 2 are continuous along the coast, through the gap south of Santa Rosa Island and northward along the SR-C Ridge. The dissolved oxygen deficit reaches its maximum value at this level, -14. The symmetry in the dipole eddy anomalies observed in layer 2 is absent in layer 3.

5.8.4. *Layer 4 (σ_t = 26.6 to 26.9).* The middepth of layer 4 (not shown) lies between 300 and 400 m. The pattern of the spiciness anomaly is very similar to that for layer 3, differing only in that the anomalies are slightly greater in the gap south of Santa

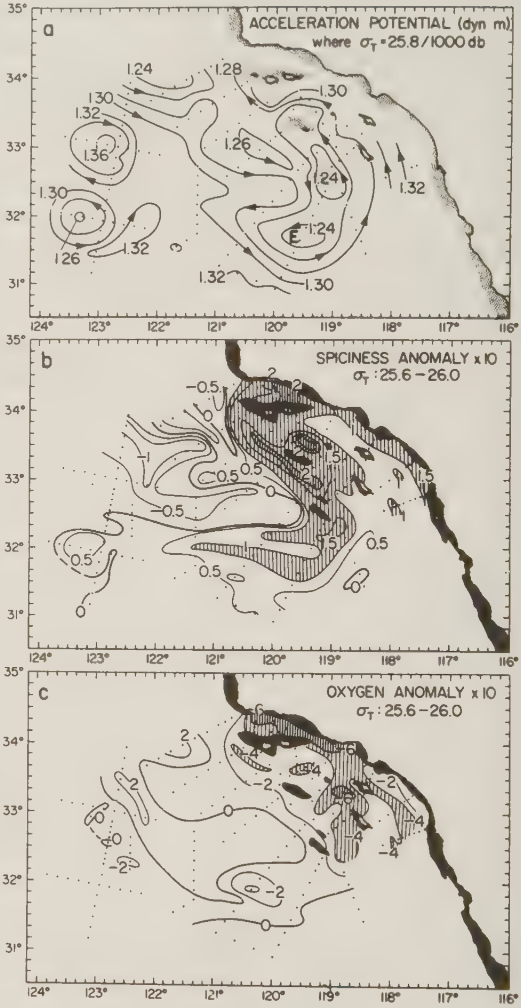

Fig. 10. (*a*) Acceleration potential (dynamic meters, or 10 $m^2 s^{-2}$) at the surface where σ_t = 25.8 relative to 1000 dbar. E denotes the center of a subsurface eddy. (*b*) Anomaly (from the 39-station mean) of spiciness × 10 units of σ_t averaged over a range in σ_t of 25.6 to 26.0 (layer 1). Positive anomalies in excess of 1 are hatched. (*c*) Anomaly of oxygen concentration × 10 mL L^{-1} as above (layer 1). Negative anomalies below -4 are hatched.

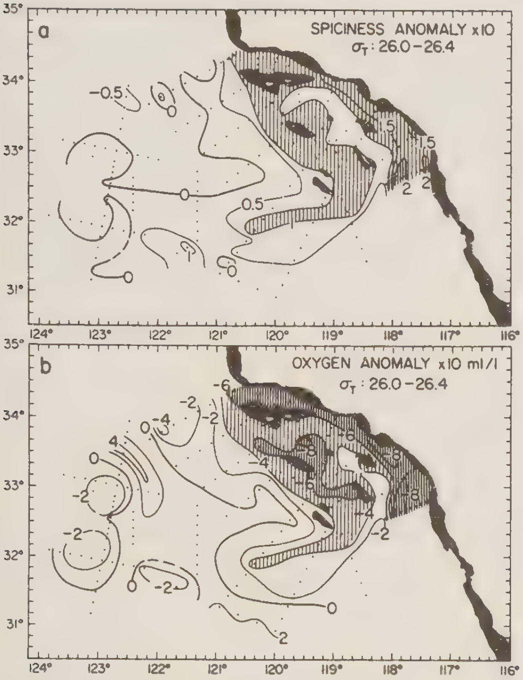

Fig. 11. (*a*) As per Figure 10*b*, except for a range in σ_t of 26.0 to 26.4 (layer 2). (*b*) As per Figure 10*c*, except for a range in σ_t of 26.0 to 26.4 (layer 2).

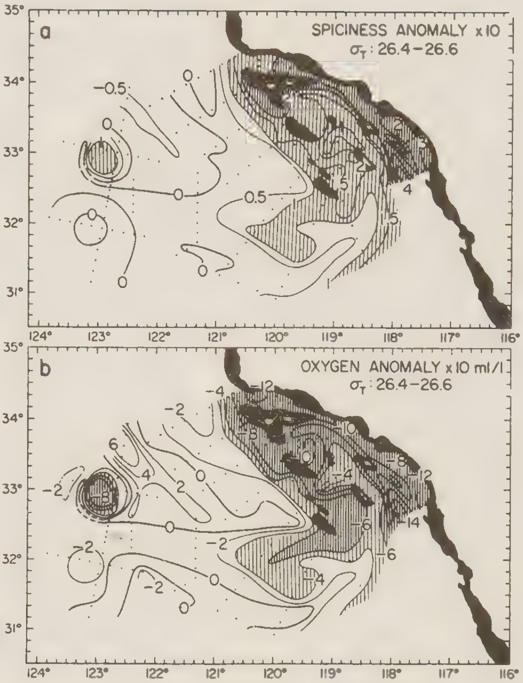

Fig. 12. (*a*) As per Figure 10*b*, except for a range in σ_t of 26.4 to 26.6 (layer 3). (*b*) As per Figure 10*c*, except for a range in σ_t of 26.4 to 26.6 (layer 3).

Rosa Island and in the offshore penetration in the northern limb of eddy E. While the overall pattern of the oxygen anomaly is similar to layer 3, the range is less than half.

6. DISCUSSION

6.1. *Path and Continuity of the California Undercurrent off Southern California*

The dynamic height at 250 m (Figures 3*a* and 6) reveals that the California Undercurrent is the strongest continuous flow at that depth. It follows the continental slope through the California Bight and exits the bight through the northernmost gap in the SR-C Ridge, and then continues poleward along the continental slope. The distributions of salinity and dissolved oxygen on the surface where $\sigma_t = 26.6$ (Figures 3*b* and 3*c*) confirm this path and the continuity of the CU. The characteristic extremes of relatively high salinity (hence relatively high temperature) and low oxygen and the decrease in their values along the path indicated by the dynamic height identify the waters as being of southern origin. The dynamic height patterns at 250 m suggest that there is poleward flow throughout much of the remainder of the bight, although at lesser speeds, and that there is westward flow out of each of the gaps. Mixing with waters that enter the bight from offshore sources reduces the extreme values of water characteristics in the more southerly gaps.

The density surface of 26.6 lies below the sill depth of the eastern entrance of the Santa Barbara Channel. Hence this surface does not show flow of the CU within the Santa Barbara Channel. At lesser densities the channel is open to flow (Figures 10, 11, and 12). Other data [*Kolpack and Drake*, 1985] provide additional evidence for a poleward, subsurface flow through the Santa Barbara Channel. We presume that the volume flow of the CU through the SR-C Ridge is considerably greater than that through the Santa Barbara Channel because of the greater restriction to flow imposed by the eastern entrance to the channel.

6.2. *Contrast of California Undercurrent Flow With Near-Surface Flow*

The CU is identified in section II of Figure 5 by the subsurface maxima in poleward geostrophic velocity found at intermediate depths within the San Pedro Channel (>0.12 to >0.24 m s^{-1}), immediately to the west of Santa Catalina Island (>0.06 m s^{-1}) and to the northwest of Tanner Bank (>0.12 m s^{-1}). The poleward flow is, in fact, continuous across the bight at these depths. In the southern part of its path through the bight, the strong core of the CU underlies a weak, spatially incoherent coastal surface flow (Figure 2*a*). In the northern part of the bight and in the northernmost gap in the SR-C Ridge the CU underlies strong surface flow that is coincident in direction and associated with the northern limb of the SCE. Westward, beyond the gap, the CU turns poleward (Figure 6) while the surface flow divides (Figure 2*a*); the major portion of this surface flow is retained in the SCE.

Although there is a general correspondence of poleward flow in the bight between the sea surface and 250 m, there is considerable difference with depth in the detail of the patterns of flow. In a matter of some tens of meters below the surface, circulation patterns change (Figures 2*a* and 10*a*). Near 50-m depth a greater portion of the flow exiting the northern gap turns poleward, and the center of the SCE shifts southward from San Nicolas Island to Cortes Bank. Eddy E enlarges and intensifies with increasing depth, while the SCE weakens (Figures 10*a* and 6). At 250 m there is only a vestige of the SCE flow about Cortes Bank.

The CU is both a narrow energetic subsurface poleward flow concentrated over the continental slope and a broad weak poleward transport found out to 200 km from the coast. The offshore CC is regarded as a relatively shallow flow [*Reid et al.*, 1958]. The present data show that at 250 m the continuity of the CC is replaced by largely eddylike flow (Figure 6). At this depth the dynamic height indicates that much of the waters from the north and northwest turn about and join the CU at various latitudes.

6.3. *Correspondence of Velocity and Anomaly Patterns*

There is a general correspondence between the high values of subsurface poleward flow (section II, Figure 5) and high values of positive spiciness anomaly and negative oxygen anomaly (section II, Figure 9). The anomalies are greatest nearest the continental slope and, at slightly lesser values, are found in a layer at intermediate depths across the bight and immediately westward of the SR-C Ridge. Both the velocity structure and the anomaly patterns indicate the presence of a branch of the CU to the northwest of Tanner Bank. This finding is supported by the pattern of dynamic height at 250 m (Figure 6) where a contour labeled 0.8 dyn m passes San Clemente Island, exits the bight through a gap north of Tanner Bank, and continues poleward. A similar correspondence of flow and anomaly patterns is evident west of San Miguel Island (section I, Figures 5 and 9).

An exception to the correspondence of patterns of extrema in velocity and anomalies occurs over the continental slope in section II, Figure 5. The velocity maximum there (0.24 to 0.28 m s^{-1}), at 65-m depth, is well above the depths of the extrema in anomalies and appears to be recirculation of mixed waters within the bight.

Of the two additional bodies of strong subsurface poleward flow in section II, Figure 5, the one at a distance of 250 km from the coast is associated with anomalously spicy and low-oxygen water, and the other at 340 km is not (Figure 9). The one located at 250 km is a part of eddy E (Figure 6). At 250-m depth the geostrophic velocity perpendicular to this section is 0.11 to 0.12 m s^{-1} in both limbs of eddy E. The subsurface velocity maximum located at 340-km distance appears to be an eddy or meander carrying typical CC waters. This feature is too close to the edge of the station grid to be resolved by these data.

6.4. *The Lateral Spread of CU Waters*

The four density layers chosen for the analysis of water characteristics can be seen to encompass the range of depth of the layers of anomaly extremes (Figure 9). In the following discussion they are taken in sequence starting with the surface domain and layer 1.

Eddy-induced upwelling and divergence within the cyclonic SCE disperses surface waters so as to eliminate the subsurface salinity minimum (Figure 2*b*) and bring relatively high salinity waters to the surface. The doming of the salinity structure within the SCE and near-surface turbulent mixing enhances the downward transport of heat from the surface and produces an isolated maximum in spiciness anomaly in layer 1 (Figure10*b*). Wind-induced upwelling combined with surface heat exchange and vertical mixing may also account for the greater spiciness of this layer in the Santa Barbara Channel and in the coastal strip. The northward penetration within the center of the bight of water with spiciness anomalies of <1 separates the effects of coastal events from those of the SCE. The tongue of values greater than 0.5 that projects offshore from the southern end of the SR-C Ridge must have formed as a result of offshore transport. Eddy E is relatively well defined at this level (approximately 70 m). Further, the western part of the tongue lies between 100 and 140 m and underlies the southeast transport of the low-salinity core of the CC. In layer 1 the spatial patterns of the anomalies of spiciness and dissolved oxygen do not match, especially within the bight. This condition suggests that local near-surface processes, including biological processes, and vertical exchange have a significant effect upon the distributions and lateral transport has a minor role.

Layer 2 encompasses a vertical minimum in spiciness anomaly over most of the survey area (Figure 9). The minimum is maintained by southward and onshore transport of CC waters which are relatively isolated from the most immediate effects of near-surface processes. Only within the coastal strip does the minimum lie above layer 2. The relatively large spiciness anomaly, >2, and large oxygen anomaly, <-8, entering the grid from south of San Diego at approximately 122 m is the upper part of the CU water mass. The similarity of the patterns of the anomalies, their close match to the pattern of acceleration potential (shown only for layer 1), and the downstream gradation of these values from off San Diego along the general path of flow, all point toward lateral transport as the primary determinant of these patterns.

The magnitude of the anomalies in layer 3 (Figure 12) is about twice that of layer 2. The oxygen anomaly, in particular, has its largest range of extremes in layer 3, from 6 in the CC waters entering from the northwest to -14 in the CU waters entering from the southeast. This large range provides the strongest development of the characteristic pattern of anomaly distribution, and this is the best of the four layers for tracing the flow of the CU. A core of large values of positive spiciness anomaly and negative oxygen anomaly, which gradually diminish along its path, follows the continental slope northward, across the bight south of the Channel Islands and out through the northern gap in the SR-C Ridge where it turns northward again. Moderately large values of anomalies also continue southward along the SR-C Ridge, then offshore in a tongue projecting westward from the southern end of the ridge. CC waters from the north, identified by anomalies of opposite sign to those of the CU, enter the grid from the northwest. Waters of intermediate anomaly values penetrate the center of the bight as they do in shallower layers, but they have assumed more of the characteristics of CU water in this layer. Large values of anomalies, indicative of CU waters, also continue into the Santa Barbara Channel (which is open on its eastern end for most (but not all) of the depth range of layer 3.

Layer 4 encompasses the deeper portion of CU water as identified by water mass characteristics (Figure 9). The distribution patterns of anomalies are much the same as those in the overlying waters.

6.5. *Eddy E*

The SCE is a shallow eddy with its maximum velocities at the surface, whereas eddy E is deeply rooted with its maximum velocities at depths greater than 200 m. It does not appear, therefore, that these features have a direct association. Rather, eddy E appears to have developed from baroclinic instabilities that are centered in the depth range of the CU. The patterns of geostrophic circulation and anomalies provide strong evidence that baroclinic instabilities develop in the CU at this locale as a result of the presence of the large bathymetric features in the SR-C Ridge. The configuration of eddy E and the offshore protrusion of waters of CU origin indicate a major offshore discharge of subsurface waters of near-coastal origin toward the region of the eddy dipole.

At a position 250 km offshore in section II of Figure 5 there is a maximum in geostrophic velocity (>0.18 m s^{-1}) at a depth of 550 m. The position of this finding, 32°08′N, 120°08′W, falls between the northern limb of eddy E and the southern limb of an adjacent small anticyclonic eddy. At a depth of 500 m, the dynamic height relative to 1000 dbar (Figure 13) shows, in fact, that eddy E is relatively weak and the anticyclonic eddy is strong.

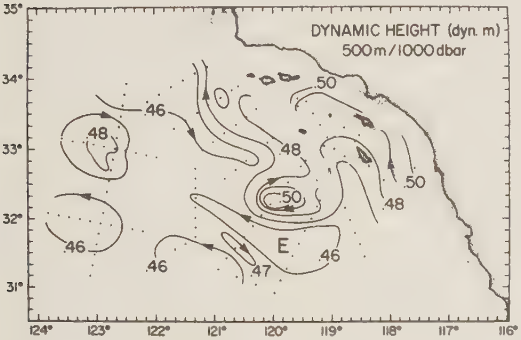

Fig. 13. Dynamic height (dynamic meters, or 10 m^2 s^{-2}) at 500 m relative to 1000 dbar.

The line of stations that comprises section II (Figure 1) misses the center of eddy E (Figure 6). The geostrophic velocity section for the line of stations that does bisect eddy E (not shown) demonstrates that the maximum in rotational velocity of eddy E occurs between 200 and 250 m, a range of depth that includes the maxima in the anomalies of spiciness and oxygen. At 500 m and below, the SR-C Ridge appears as an unbroken submerged peninsula. Flow at 500 m (Figure 13) appears to enter the bight from the south along the continental margin. It must exit the bight around the southern end of the SR-C Ridge, in the vicinity of the deep anticyclonic eddy. The anticyclonic eddy, by virtue of its proximity to the SR-C Ridge and its spatial scale, may also have been created by a bathymetrically induced instability in flow.

6.6. *Offshore Transport of CU Waters*

The offshore transport of CU waters that these survey data reveal is likely episodic in nature. Therefore this single realization of flow and water mass distribution does not permit definitive conclusions as to its development and evolution. Our findings combined with background information do, however, provide some evidence as to the probable turn of events. In the vicinity of the international border the seasonally averaged CU attains its minimum strength (or disappears altogether) during April and undergoes its greatest increase during June and July [*Lynn and Simpson*, 1987]. We reason that the effect of the impediment of the SR-C Ridge on the CU is greatest during this period of seasonal intensification of baroclinic flow. The possible accumulation of CU waters at depth within the bight because of the constriction of the gaps in the ridge would ultimately lead to the discharge of these waters around the southern end of the ridge. Interaction of the offshore discharge of CU waters with the offshore flow field could produce a feature like eddy E as well as the deeper anticyclonic eddy noted in Figure 13.

CU-derived waters form the core of the anticyclonic member of the eddy dipole [*Simpson and Lynn*, this issue]. This concentration of anomalous waters within the anticyclonic member of the eddy dipole suggests that this system was generated near the continental slope. The patterns of subsurface anomalies indicate a path between the southern end of the SR-C Ridge and the eddy dipole (Figures 11 and 12). *Simpson et al.* [1984] also found waters of CU origin within a monopole eddy in nearly the same location as the anticyclonic member of the dipole. These findings imply that undercurrent dynamics play a crucial role in the development of offshore mesoscale eddies. The patterns found in July 1985 provide circumstantial evidence which suggests that the eddy dipole was generated off the SR-C Ridge and migrated westward to its offshore position, leaving in its wake mixed waters which included some CU waters. A recurrent mesoscale eddy found off Sitka, Alaska, also contains waters within a similar depth–density realm that have characteristics indicating an origin of the shelf–slope region [*Tabata*, 1982] and similar observations were made of an eddy off Oregon in early 1978 [*Huyer et al.*, 1984]. A mathematical model of the Sitka eddy [*Swaters and Mysak*, 1985] suggests that it is bathymetrically induced.

6.7. *Depth Offset of Extremes in Anomalies of Spiciness and Oxygen*

The relationship between the spiciness anomaly and oxygen anomaly is represented in Figure 14 by vertical traces for station 42, located immediately west of Santa Catalina Island (see Figure 7). The previously defined four density layers are indicated by five ticks on the zero axis. Below 60 m and at densities greater than 25.8 there is a strong negative correlation between the anomalies as expected for CU waters. Above 60 m the correlation is positive. This break point occurs at about the bottom of the thermocline–pycnocline and indicates the depth of penetration of

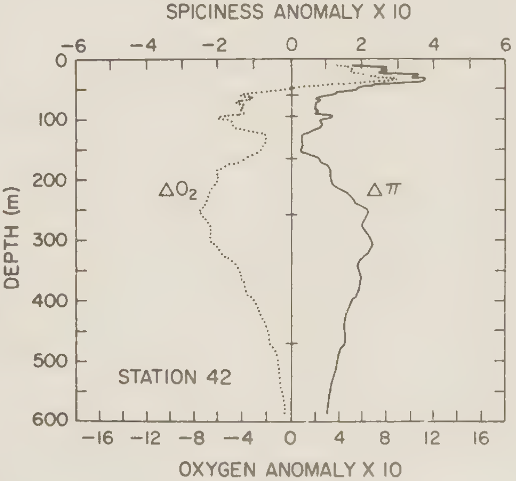

Fig. 14. Vertical profiles of the anomalies of spiciness ($\Delta\pi$) and dissolved oxygen (Δ O_2) from the 39-station mean for station 42 (west of Santa Catalina Island).

local exchange processes and strong vertical mixing. At some other stations, especially those in the SCE, the break point falls well into layer 1. At depths below this break point, large-scale transport and lateral mixing predominate. The negative correlation of anomalies is seen both in general form and in detail on a scale of 10 m. There is, however, a decreasing trend with increasing depth in the ratio of oxygen anomaly to spiciness anomaly. This trend causes the maximum oxygen anomaly to occur at a shallower depth than that for the spiciness anomaly. This trend most likely is simply a consequence of basic differences in the vertical distributions of spiciness and dissolved oxygen of the CC and CU source waters.

6.8. *Comparison of July 1985 With Long-Term Mean*

In order to compare our results for July 1985 with the long-term mean (LTM), we used the 29-year mean July values of temperature, salinity, and dissolved oxygen for CalCOFI line 90 [*Lynn et al.*, 1982] to compute spiciness and the anomalies of spiciness and dissolved oxygen from the 39-station spatial mean. The vertical sections of these anomalies (Figure 15) have a vertical exaggeration 8 times greater than for those presented earlier (Figures 5 and 9). Section II of Figure 9 nearly aligns with CalCOFI line 90 and extends westward to station 80. The full westward extent of the July 1985 grid reaches 570 km offshore, a position between CalCOFI stations 100 and 110, and the locale of the 39 stations used to create the mean CC characteristics falls in the region of CalCOFI stations 60 to 90. The patterns of the LTM anomalies (Figure 15) are very similar to those found in 1985 (Figure 9). In particular, in the LTM as in 1985, waters having anomalies >1 in spiciness and <-3 in oxygen extend 300 km offshore within layers 3 and 4; maximum values (>3 in spiciness and <-9 in oxygen) appear in the San Pedro Channel at about depths of 250 to 300 m. Spiciness is high in the surface waters, especially near the SR-C Ridge (CalCOFI station 53), where high values penetrate downward into layer 1. Also, there is an intermediate layer where spiciness is a minimum. Thus conditions observed in 1985 can be accepted as typical of the mean, especially the offshore extension of waters that carry a strong complement of CU characteristics.

Between 300 and 500 m at CalCOFI station 100, there is a separate body of water having anomalies >1 in spiciness and <-3 in oxygen (Figures 15*a* and 15*b*). This station is very near the location of the dipole eddy system. The vertical section of LTM July geostrophic velocity [*Lynn et al.*, 1982, plate on page 153] corresponding to the LTMs of temperature and salinity demonstrates a pattern of flow including a weak reversal that associates it with the separate body of anomalous water. Taken together, these findings strongly suggest that this separate feature is a subsurface signature of recurrent mesoscale eddies. Thus the findings attest to the recurrent nature of offshore mesoscale eddies at preferred locations [*Simpson et al.*, 1984, 1986; *Lynn and Simpson*, 1987] and strongly suggest that the offshore transport and eddy entrainment of CU-derived waters [*Simpson and Lynn*, this issue] is a common feature of the CCS.

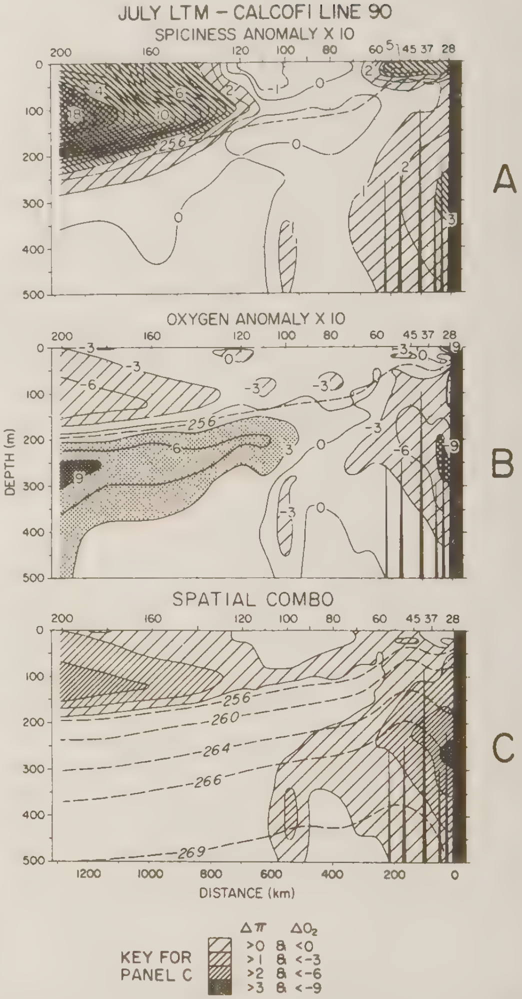

Fig. 15. (*a*) Vertical section of the anomaly of the long term mean (LTM) July spiciness for CalCOFI line 90 from the 39-station spatial mean. Various densities of hatching are used for values of 1–3, 3–15, and >15. (*b*) The same as Figure 15*a*, except for oxygen. Values >3 and <-3 are lightly shaded; values >9 and <-9 are heavily shaded. (*c*) The spatial combination of positive spiciness (π) anomaly and negative oxygen anomaly from Figures 15*a* and 15*b*. Contours are identified in key. Shading intensities grade accordingly.

6.9. *Comparison With North Pacific Eastern Central Waters*

To the west, the North Pacific Eastern Central waters have anomalies of spiciness and dissolved oxygen which clearly differentiate them from CC and CU waters (Figures 15*a* and 15*b*). The distinguishing features of CU waters are emphasized in Figure 15*c*, in which all waters that have a combined positive spiciness anomaly and a negative oxygen anomaly are shaded. The density of shading is stepped for combinations of anomaly values as given in the key. The maximum step, spiciness >3 and oxygen <-9, appears only over the continental slope between depths of 230 and 300 m. Within our chosen density layers there is no second source of waters having the same mean combination of characteristics as CU waters. (Seasonal and nonseasonal variations and dynamic events about the California Front, however, may occasionally produce such waters within layer 1.) Thus the anomaly structures provide unambiguous evidence that both eddy E and the offshore eddy dipole contain CU waters. Necessarily, this implies a subsurface offshore transport mechanism.

7. CONCLUSIONS

1. The California Undercurrent transports spicy (warm and saline), low-oxygen waters poleward through the California Bight. The subsurface velocity core of this current is associated with vertical and lateral extremes in water characteristics that are readily defined by their anomalies from California Current waters. In July, at least, these extreme values of anomalies occur at or near $\sigma_t = 26.6$ and a depth of 275 m over the continental slope. The core, thus defined by flow and water characteristics, follows the continental slope within the bight, turns westward along the slopes south of the Channel Islands, exits the bight in the northernmost gap of the Santa Rosa–Cortes (SR-C) Ridge, and then turns northward. At levels above the sill depth of the eastern end of the Santa Barbara Channel (230 m) and at densities somewhat less than $\sigma_t = 26.6$, a branch of the CU continues northward along the continental slope into the Santa Barbara Channel.

2. At intermediate depths, typical of the CU, considerable portions of the CC waters turn cyclonically, mix with CU waters and join the CU. Thus there is both an energetic narrow core of poleward flow along the continental slope and a broad, somewhat slower, poleward flow that extends offshore to distances of the order of 100 to 150 km.

3. In July 1985 the flow within the bight was almost everywhere poleward. Branches of the CU in which its waters were diluted with offshore waters exited the bight through several gaps in the SR-C Ridge and merged again in a poleward flow. Part of the CU was diverted about the southern end of the ridge. There, eddying flow carried waters having a large component of CU water characteristics westward beneath the CC.

4. Waters of CU origin are transported offshore beneath the CC and are found in the offshore mesoscale eddy system [*Simpson and Lynn*, this issue]. This transport appears to result from baroclinic instabilities in the CU caused by the bathymetry and the seasonal intensification of flow. Distorted eddy-like features near the southern end of the SR-C Ridge are one manifestation of the baroclinic instabilities. The flow patterns of these features closely correspond to the distribution patterns of CU water characteristics, and together they indicate the path of offshore transport to the offshore mesoscale eddy field.

5. Circumstantial evidence suggests that the eddy dipole was generated off the SR-C Ridge and migrated westward.

6. The major aspects of the conditions found in July 1985 also appear in the long-term mean for July, including the magnitude and distribution of CU water characteristic anomalies, the association of these anomalies with the density field, and the entrainment of CU waters into the offshore mesoscale eddy system. Thus the findings for July 1985 appear to be typical conditions.

7. Long-term means of water characteristics in the eastern North Pacific show that the combination of relatively high spiciness and low dissolved oxygen uniquely define CU waters at densities greater than $\sigma_t = 26$ in the California Current system.

8. In some instances, a reference pressure of 500 dbar for the calculation of dynamic height off California does not provide an adequate representation of the strength and pattern of geostrophic flow. A very active pattern of geostrophic flow was observed at 500 m referred to 1000 dbar in July 1985.

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REFERENCES

Allen, W. E., Vernal distribution of marine plankton diatoms offshore in southern California in 1940, *Bull. Scripps Inst. Oceanogr.*, *5*, 335–369, 1945.

Chelton, D. B., Seasonal variability of alongshore geostrophic velocity off central California, *J. Geophys. Res.*, *89*, 3473–3486, 1984.

Davis, R. E., Drifter observations of coastal surface currents during CODE: The method and descriptive view, *J. Geophys. Res.*, *90*, 4741–4755, 1985.

Hickey, B. M., The California Current system—hypotheses and facts, *Prog. Oceanogr.*, *8*, 191–279, 1979.

Huyer, A., R. L. Smith, and B. M. Hickey, Observations of a warm-core eddy off Oregon, January to March 1978, *Deep Sea Res.*, *31*, 97–117, 1984.

Kolpack, R. L., and D. E. Drake, Transport of clays in the eastern part of Santa Barbara Channel, Calif. *Geo. Mar. Lett.*, *4*, 191–196, 1985.

Lynn, R. J., and J. J. Simpson, The California Current system; The seasonal variability of its physical characteristics, *J.Geophys. Res.*, *92*, 12,947–12,966, 1987.

Lynn, R. J., K. A. Bliss, and L. E. Eber, Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-*t*, stability, dynamic height, oxygen and oxygen saturation in the California Current, 1950–1978, *CalCOFI Atlas 30*, 513 pp., State of Calif. Mar. Res. Comm., La Jolla, 1982.

Montgomery, R. B., A suggested method for representing gradient flow in isentropic surfaces, *Bull. Am. Meteorol. Soc.*, *18*, 210–212, 1937.

Montgomery, R. B., Transport of the Florida Current off Habana, *J. Mar. Res.*, *4*, 198–219, 1941.

Montgomery, R. B., and E. D. Stroup, Equatorial waters and currents at 150°W in July–August 1952, *Johns Hopkins Oceanogr. Stud.*, *1*, 68 pp., 1962.

Munk, W., Internal waves and small-scale processes, in *Evolution of Physical Oceanography*, edited by B. A. Warren and C. Wunsch, pp. 264–291, MIT Press, Cambridge, Mass., 1981.

Owen, R. W., Eddies of the California Current system: Physical and ecological characteristics, in *The California Island: Proceedings of a Multidisciplinary Symposium*, edited by D. Power, 787 pp., Santa Barbara Museum of Natural History, Santa Barbara, Calif., 1980.

Reid, J. L., Jr., Measurements of the California Countercurrent at a depth of 250 m, *J. Mar. Res.*, *20*, 134–137, 1962.

Reid, J. L., and A. W. Mantyla, The effect of the geostrophic flow upon coastal sea elevations in the northern North Pacific Ocean, *J. Geophys. Res.*, *81*, 3100–3110, 1976.

Reid, J. L. Jr., G. I. Roden, and J. G. Wyllie, Studies of the California Current system, *CalCOFI Rep.*, *6*, pp. 27–56, Calif. Coop. Oceanic Fish. Invest., La Jolla, 1958.

Reid, J. L., Jr., E. Coughran, and C. Worral, Detailed measurements of a shallow salinity minimum, *J. Geophys. Res.*, *69*, 4767–4771, 1964.

Shepard, F. P., and K. O. Emery, Submarine topography off the California coast: Canyons and tectonic interpretations, *Spec. Pap. Geol. Soc. Am.*, *31*, 171 pp., 1941.

Simpson, J. J., and R. J. Lynn, A mesoscale eddy dipole in the offshore California Current, *J. Geophys. Res.*, this issue.

Simpson, J. J., T. D. Dickey, and C. J. Koblinsky, An offshore eddy in the California Current system, I, Interior dynamics, *Prog. Oceanogr.*, *13*, 5–49, 1984.

Simpson, J. J., C. J. Koblinsky, J. Peláez, L. R. Haury, and D. Wiesenhahn, Temperature—plant pigment—optical relations in a recurrent offshore mesoscale eddy near Point Conception, California, *J. Geophys. Res.*, *91*, 12,919–12,936, 1986.

Stommel, H., On the cause of the temperature-salinity curve in the oceans, *Proc. Natl. Acad. Sci., U.S.A.*, *48*, 764–766, 1962.

Sverdrup, H. U., and R. H. Fleming, The waters off southern California, March to July 1937, *Bull. 4*, pp. 261–378, Scripps Inst. of Oceanogr., Univ. of Calif., La Jolla, 1941.

Swaters, G. E., and L. A. Mysak, Topographically-induced baroclinic eddies near a coastline, with application to the northeast Pacific, *J. Phys. Oceanogr.*, *15*, 1470–1485, 1985.

Tabata, S., The anticyclonic, baroclinic eddy off Sitka, Alaska, in the northeast Pacific Ocean, *J. Phys. Oceanogr.*, *12*, 1260–1282, 1982.

Wooster, W. S., and J. H. Jones, California Undercurrent off northern Baja California, *J. Mar. Res.*, *28*, 235–250, 1970.

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Serum Lipoproteins in Striped Bass (*Morone saxatilis*): Effects of Starvation

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Withholding food for 4 wk resulted in more extensive alterations within serum lipoprotein classes in striped bass (*Morone saxatilis*) than were evident in serum total lipids where only a decrease in triglycerides was significant. Total serum lipoprotein concentrations were about 3300 mg/dL in both fed and starved fish; however, high density lipoproteins (HDL) increased and very low density lipoproteins (VLDL) decreased significantly in the starved group. Quantitatively, the greatest changes in VLDL, the primary transporter of triglycerides, were declines in triglycerides and cholesterol esters. Within low density lipoproteins, triglycerides and phospholipids decreased. The HDL composition was affected least by starvation. Phospholipids were the dominant lipid in HDL and increased from 479.1 mg/dL in fed to 670.2 mg/dL in starved fish. The apoproteins of each lipoprotein class changed little qualitatively due to starvation. Our results reflect the importance of maintaining high levels of lipoproteins as a transport system for lipids from storage depots to depleted tissues permitting survival during prolonged periods of starvation that are often encountered by fish during colder months and during spawning migrations. Furthermore, during starvation HDL appears to assume increased significance as a vehicle for the transport of structural lipids to maintain tissue integrity.

La privation de nourriture pendant quatre semaines a produit des altérations plus importantes dans les classes de lipoprotéines sériques chez le Bar d'Amérique (*Morone saxatilis*) qu'il ne paraissait dans les lipides sériques totaux, ce qui n'avait révélé de baisse importante que dans la teneur en triglycérides. La concentration en lipoprotéines sériques totales était d'envirion 3300 $mg \cdot dL^{-1}$ chez les sujets nourris ainsi que les sujets affamés. Cependant, la teneur en lipoprotéines de haute densité (HDL) a augmenté alors que celle des lipoprotéines de très basse densité (VLDL) a diminué significativement chez les sujets affamés. Sur le plan quantitatif, les plus importants changements en VLDL, le principal vecteur des triglycérides, a été la diminution en concentration des triglycérides et des esters du cholestérol. Quant aux lipides de basse densité (LDL), la teneur en triglycérides et en phospholipides a diminué. La composition en HDL a le moins varié par suite du traitement. Les phospholipides constituaient la principale forme de HDL et leur concentration est passée de 479,1 $mg \cdot dL^{-1}$ chez les sujets nourris à 670,2 $mg \cdot dL^{-1}$ chez les sujets affamés. Les apoprotéines de chaque classe de lipoprotéines ont peu varié qualitativement par suite de l'inanition. Nos résultats montrent l'importance de garder les lipoprotéines à un niveau élevé comme moyen de transport des lipides, des réserves aux tissus qui se sont appauvris, ce qui assure la survie durant les périodes prolongées de famine que les poissons doivent souvent affronter durant les mois d'hiver et au cours des migrations pour la reproduction. En outre, le HDL associé à l'inanition semble gagner en importance comme vecteur pour le transport des lipides structuraux en vue de conserver l'intégrité des tissus.

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Fish have an impressive ability to withstand long periods of starvation. This capacity is adaptive since many species of fish are subjected to natural periods of starvation or very low food intake during spawning or cold months of the year in temperate latitudes when prey abundance is low (Love 1970). Energetic demands are met primarily by lipid oxidation in fish (Cowey and Sargent 1979) and this is particularly true during starvation (Shul'man 1972).

Lipids are stored in substantial quantities in various tissues, including muscle, liver, and mesenteric depots, and, in addition to being a source of energy, provide components for membrane synthesis and precursors of steroid hormones. Many studies have shown that fish mobilize energetic lipids (e.g. triglycerides) from tissues preferentially to structural lipids (e.g. phospholipids) during starvation, but phospholipids are mobilized if starvation is prolonged (reviewed by Love 1980; Henderson and Tocher 1987). Since a basic minimum of energy and structural integrity of tissues must be maintained for survival, lipids must be supplied to depleted tissues from storage depots. Beyond these needs for maintenance, substantial quantities of energetic and structural lipids must be supplied to gonads, especially ovaries, during reproductive development. In anadromous species which undergo lengthy spawning migrations without feeding, gonadal development is dependent to a large extent on the transport of stored lipids (Henderson and Tocher 1987).

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Lipids are transported in blood serum complexed with specific proteins (apolipoproteins) as particles known as lipoproteins. Serum lipoproteins are routinely characterized by size, density, and their chemical composition. In ascending order of density, they are chylomicrons, very low density (VLDL), low density (LDL), and high density (HDL) lipoproteins. Although studied rather extensively in birds and mammals, serum lipoproteins have been described in only a few species of fish (Chapman 1980), most notably rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981). A common feature of serum lipoproteins in teleost species studied to date is that they are found in very high concentrations relative to birds and mammals (Chapman 1980). Moreover, during the prespawning period HDL appears to become elevated in rainbow trout (Fremont and Marion 1982) and pink salmon (Nelson and Shore 1974).

From the above observations, assessing changes in serum lipoproteins during starvation may reveal which components are most significant for maintenance of tissue integrity and synthesis. Black and Skinner (1986) found that starvation produced changes in cholesterol concentrations in serum lipoproteins of rainbow trout. However, there are no published reports on the effects of fasting on the lipid and protein compositions of serum lipoproteins in fishes. To investigate this, a study was conducted to determine the changes in the composition and concentration of serum lipoprotein classes of starved striped bass (*Morone saxatilis*), an anadromous species that experiences periods of starvation during winter months and during spawning (Woodhull 1947; Stevens 1966; Jones and Sidell 1982).

Materials and Methods

Adult striped bass (4-yr-old, mean FL 47 ± 15 cm) were collected in June 1983, after the spawning period, from the San Francisco Bay estuary by gill net and transported to a 20 000-L raceway using an aerated mobile fish transporter. They were acclimatized in the raceway to ambient, filtered bay water (approximately 17°C and 25 ‰ salinity) for 2 wk prior to randomized placement in the experimental tanks. All fish were fed anchovies on alternate days while in the raceway. Each circular 3200-L fiberglass experimental tank contained six fish and received flow-through ambient filtered bay water (approximately 18.5°C and 27 ‰ salinity) under the natural photoperiod. During the 4-wk experimental period, fish in one of the tanks were fed anchovies daily until satiated whereas no food was provided to fish in the other tank.

Blood was obtained by cardiac puncture using sterile Vacutainers[3] without anticoagulant and allowed to clot prior to centrifugation and serum withdrawal. After separation, each serum sample received antibacterial agents (0.001% sodium merthiolate and 0.01% sodium azide) and 1 mg/mL EDTA. Samples were stored at −80°C under nitrogen until analyzed.

Isolation of Lipoproteins

Serum lipoproteins were separated by sequential ultracentrifugation into density classes routinely used for human lipoprotein isolation for comparative purposes with studies of fishes and other animals. The density intervals employed were; $d<1.0063$ g/mL for VLDL, $1.0063<d<1.063$ g/mL for LDL, and $1.063<d<1.21$ g/mL for HDL. Appropriate density salt solutions for ultracentrifugal isolation of lipoprotein classes were prepared with NaCl and NaBr in deionized water and checked by pycnometry according to Lindgren (1975). All salt solutions contained antibacterial and antioxidation agents at the same concentrations as in serum samples. Since the nonprotein density of striped bass serum was unknown, it was adjusted to 1.0063 g/mL by exhaustive dialysis with a NaCl solution of $d=1.0063$ g/mL prior to lipoprotein fractionation.

Lipoprotein fractions were isolated by the sequential ultracentrifugation techniques described in detail by Lindgren (1975) using a Beckman L5-75 with a 50-Ti rotor at 10°C. Briefly, 2.0 mL of dialyzed serum was added to a polycarbonate centrifuge tube and mixed with 4.0 mL of d 1.0063 g/mL NaCl solution and spun at 45 000 rpm (135 000 × g) for 18 h. The top 1.0 mL containing VLDL and the next 1.0 mL background fraction were removed. The remaining solution's density was raised to 1.063 g/mL with 2.0 mL of the appropriate density NaCl–NaBr solution and centrifuged for 20 h at 45 000 rpm (135 000 × g). The top 1.0 mL containing LDL and the next 1.0 mL for background assessment were removed. The remaining infranatant was increased in density to 1.21 g/mL with 2.0 mL of a NaCl–NaBr solution and spun at 45 000 rpm (135 000 × g) for 40 h at 10°C. As before, the top 1.0 mL containing HDL was removed as well as the next 0.5 mL for background.

Lipid Composition Analysis

Lipids were extracted from aliquots of serum and lipoprotein fractions with 2 × 15 volume of ethanol–ether (3:1). Precipitated protein was removed by centrifugation and the supernatant was evaporated under a stream of nitrogen. The dried lipid residue was reconstituted with chloroform–methanol (1:1) and analyzed for total lipid (Harvey and Patton 1981) and lipid class composition in triplicate using an Iatroscan TH-10 analyzer (Iatron Laboratories, Inc., Tokyo, Japan). The S-II Chromarods were developed in a solvent system of hexane–ethyl ether–acetic acid (95:5:0.2) which resolves triglycerides, alkyl esters/glyceryl ethers, free cholesterol, cholesterol esters, and phospholipids. Triglycerides were also determined in lipoprotein fractions and background fractions by the enzymatic method of Bucolo and David (1973).. Lipid-containing solutions were always stored in Teflon-lined screw-capped culture tubes under nitrogen in the dark at −20°C between procedural manipulations.

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[3] References to trade names does not imply endorsement by the National Marine Fisheries Service.

TABLE 1. Total concentrations of lipid components and protein in serum of striped bass fed or starved for 4 wk. Values represent mean ± SE of six fish expressed as mg/dL. * = significantly different from fed ($P<0.05$).

Component	Treatment	
	Fed	Starved
Triglycerides	618 ± 132	252 ± 53*
Glyceryl ethers/alkyl esters	150 ± 60	189 ± 88
Cholesterol esters	240 ± 46	231 ± 48
Free cholesterol	201 ± 28	202 ± 29
Phospholipids	961 ± 118	859 ± 163
Total lipids	2169 ± 215	1733 ± 298
Protein	4067 ± 228	4433 ± 208

Apoprotein Analysis

Total protein concentrations in serum, lipoprotein fractions, and background fractions were determined by a modified Lowry method for lipoprotein samples, which incorporated sodium dodecyl sulphate into the alkali reagent, allowing direct assay without delipidation (Markwell et al. 1981). Bovine serum albumin standards were employed.

Apoproteins within each lipoprotein fraction were separated and characterized by molecular weight according to the sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) method of Laemmli (1970). Samples of apo-VLDL, apo-LDL, and apo-HDL were applied to separate gels to resolve high and low molecular weight apoproteins. High molecular weight apoproteins were separated using a 3.0% monomer stacking gel atop a 5.0% separation gel and low molecular weight proteins were resolved with a 5.0% monomer stacking gel and a 10.5% separation gel. Proteins were fixed and stained in a 0.1% Coomassie Brilliant Blue solution in 50% acetic acid, prepared fresh daily. Gels were destained by repeated washings in 7% acetic acid, dried, and scanned in a Helena ''Fluor-vis'' densitometer (Helena Laboratories, Inc., Beaumont, TX) equipped with a 560-nm filter. The molecular weight of each electrophoretic band was determined by comparing its mobility with that of a series of SDS-PAGE protein standards purchased from Bio-Rad Laboratories, Richmond, CA, according to the formula of Weber and Osborn (1969). Apoprotein electrophoretic bands were not quantified for reasons discussed extensively by Chapman et al. (1975).

Statistical Analysis

Differences in the lipid compositon of lipoprotein fractions and serum from fed and starved striped bass were analyzed using the paired *t*-test.

Results

Each treatment group of striped bass contained four females and two males. Statistical analysis of the data revealed no differences in lipid composition attributable to sex. Therefore, data from both sexes were combined.

Withholding food for 4 wk resulted in a 20% decrease in serum total lipids, but only the decline in triglycerides was statistically significant (Table 1). Serum triglyceride levels decreased by about 60%. Essentially no changes occurred in the concentrations of free cholesterol, cholesterol esters, and unknown compounds referred to here as glyceryl ethers/alkyl esters due to their similar mobilities on the Chromarods. The glyceryl ethers/alkyl esters fraction may contain 1-0-alkyl-diacylglycerides which have been found in other fish species (Mori et al. 1972; Kayama 1975; Mills and Taylaur 1977). Serum phospholipids were decreased by 11% and total serum protein increased by 9% in fish subjected to starvation, but neither change was statistically significant.

Mean weight percentage composition of the major lipoprotein classes revealed that starvation altered the distributions of lipids and protein in all lipoprotein fractions (Table 2). The predominant lipid in striped bass VLDL was triglyceride, accounting for about half of the lipid present in fed fish and 39% in starved fish. Protein contributed, by weight, 9.8% of the VLDL in fed striped bass. The proportion of protein in VLDL increased during the starvation period of 18.1%. This was due to a much greater depletion of lipid relative to protein in VLDL of starved fish compared with fed; the mean absolute concentrations of protein in fed and starved striped bass VLDL were approximately the same, 62.7 mg/dL and 75.0 mg/dL, respectively. Within the lipids, the quantitative decrease in VLDL triglycerides, from 445.2 mg/dL in fed fish to 159.9 mg/dL, was the major change observed due to starvation and was largely responsible for the statistically significant decrease in total lipid (Table 2). Starvation produced a greater mean percent contribution of phospholipids in VLDL due to the decreased contribution of triglycerides, despite little change in concentration (125.7 mg/dL in fed fish, 114.1 mg/dL in starved fish). Cholesterol esters were diminished six-fold and lipids within the glyceryl ethers/alkyl esters fraction four-fold in percent composition in VLDL of starved fish. The percent contribution of cholesterol to VLDL particles remained essentially unchanged.

There was a greater proportion of cholesterol, in free and esterified forms, in striped bass LDL than in other lipoprotein classes; however, triglycerides predominated in the LDL of fed fish (Table 2). Protein contributed, on a mean weight basis, a greater proportion of the LDL mass than in VLDL. Consequently, there was less lipid in LDL particles than in VLDL. In fed fish, phospholipids comprised about the same proportion of LDL as for VLDL (14.1 and 18.6%, respectively) and also on a mean concentration basis (138.4 mg/dL in LDL and 125.7 mg/dL in VLDL). There was an inverse relationship between cholesterol esters and free cholesterol in LDL compared to VLDL, with cholesterol esters predominating in LDL.

Starvation resulted in significant decreases in the mean weight percentages of triglycerides, phospholipids, and total lipid in striped bass LDL (Table 2). The other lipid components and protein increased in starved fish LDL, although the changes were not statistically significant. Compounds with chromatographic mobilities similar to glyceryl ethers and alkyl esters accounted for a greater proportion of LDL in fed and starved striped bass than in the other two lipoprotein fractions.

Phospholipids dominated striped bass HDL lipids and accounted for about 33.5% of the weight of HDL in fed and starved fish (Table 2). In concentration, however, phospholipid increased from 479.1 mg/dL in fed fish to 670.2 mg/dL in starved fish. The composition of the HDL fraction appeared to be affected the least by starvation. The only significant change occurred in the triglycerides fraction which comprised a small proportion of HDL.

Summation of all lipid components and protein concentrations within each lipoprotein class provided an estimate of the concentration of individual lipoprotein classes within each fish.

TABLE 2. Mean weight percent composition of lipid components and protein in serum lipoprotein classes of striped bass fed or starved for 4 wk. Values represent mean (SE) of six fish. * = significantly different from fed ($P<0.05$); ** = significantly different from fed ($P<0.01$); *** = significantly different from fed ($P<0.001$).

	VLDL		LDL		HDL	
Component	Red	Starved	Fed	Starved	Red	Starved
Triglycerides	50.6	38.8	27.2	6.5**	4.6	1.2***
	(9.3)	(5.6)	(4.6)	(1.1)	(0.6)	(0.1)
Glyceryl ethers /alkyl esters	4.9	1.2	9.1	15.1	0.1	0.8
	(4.2)	(1.2)	(3.4)	(3.5)	(0.1)	(0.6)
Cholesterol esters	6.9	1.1*	12.2	15.6	4.3	3.2
	(2.5)	(0.8)	(2.9)	(0.9)	(1.0)	(1.0)
Free cholesterol	10.2	11.5	8.4	11.5	2.9	2.5
	(3.5)	(8.5)	(1.2)	(5.0)	(0.3)	(0.8)
Phospholipids	18.6	29.3*	14.1	9.1**	33.4	33.9
	(4.0)	(2.1)	(1.1)	(0.8)	(1.2)	(2.8)
Total lipids	91.2	81.9*	71.0	57.8*	45.3	41.6
	(2.0)	(3.4)	(4.0)	(3.5)	(1.3)	(4.0)
Protein	9.8	18.1*	29.0	42.2	54.7	58.4
	(2.5)	(3.3)	(4.9)	(3.7)	(1.3)	(4.0)

TABLE 3. Concentrations and mean weight percent of serum lipoprotein classes in striped bass fed or starved for 4 wk. Values represent mean (SE) of six fish. *significantly different from fed ($P<0.05$; **significantly different from fed ($P<0.01$); ***significantly different from fed ($P<0.001$).

	VLDL		LDL		HDL		Σ LP
Treatment	mg/dL	wt %	mg/dL	wt %	mg/dL	wt %	mg/dL
Fed	834	25.1	938	28.0	1436	46.9	3208
	(147)	(2.0)	(175)	2.1)	(65)	(3.8)	(378)
Starved	401*	11.7***	1063	30.9	1977**	57.4*	3441
	(35)	(0.9)	(98)	(2.8)	(101)	(2.4)	(91)

Although mean total lipoprotein concentrations changed little between fed and starved striped bass, significant differences occurred within lipoprotein classes (Table 3). The HDL was the most abundant lipoprotein in striped bass serum and was significantly elevated in starved fish. Inversely, the least abundant lipoprotein, VLDL, declined significantly in concentration subsequent to starvation. This was due, primarily, to the depletion of triglycerides, and to a lesser extent by lower levels of cholesterol esters and cholesterol. The LDL comprised about 30% of the lipoproteins and the concentration remained essentially unchanged by starvation.

The apoproteins of VLDL and LDL were resolved in sodium dodecyl sulphate polyacrylamide gels of 5% monomer concentration and those of HDL in gels of 10.5% monomer (Fig. 1). Apo-VLDL displayed four bands. The predominant component remained near the origin of the separating gel and was a broad, intense band with a molecular weight greater than 250 000 daltons. The remaining bands were much narrower and fainter and contained proteins of approximately 207 000, 47 000, and 42 000 daltons. No apoproteins with molecular weights less than 42 000 were evident on any gels of apo-VLDL.

The apoproteins of LDL separated into five major bands and two bands containing trace amounts of dye-binding material. As with apo-VLDL the largest, darkest staining component had a molecular weight in excess of 250 000 daltons. Apo-LDL also contained a band at about 42 000 daltons with the same staining characteristics as seen for apo-VLDL. Other bands of similar size and intensity were observed with molecular weights of about 77 000, 60 000, and 51 000 daltons. Trace amounts of polypeptides occurred with apparent molecular weights of approximately 203 000 and 149 000 daltons.

Apo-HDL was distinctly different in composition relative to VLDL and LDL (Fig. 1). The largest and darkest staining component corresponded to a molecular weight of about 24 000 daltons. The next most prominent band had an apoprotein of 13 000 daltons. A substantial amount of material was observed with a molecular weight greater than 100 000 daltons. Other faint bands were identified with molecular weights of 76 000, 50 000, and 28 000 daltons.

Qualitatively, withholding food for 4 wk resulted in very little change in the apoprotein content of lipoproteins in striped bass. Within the resolution obtained by SDS-PAGE, all components observed on the gels for apo-HDL and apo-LDL from fed fish were present on those from starved fish. The only difference noted occurred in apo-VLDL, where the band with an estimated molecular weight of 207 000 daltons found in fed fish was absent in apo-VLDL of starved fish. Since analytical manipulations (e.g. repeated washings, dialysis, and ultracentrifugations of lipoprotein fractions) and variable chemical characteristics (e.g. differential chromogenicities to stains between electrophoresis bands) are known to compromise the validity of band quantification (Herbert et al. 1978), we did not assess apoprotein concentrations within lipoprotein fractions of fed or starved fish.

Discussion

Serum Lipids

A decrease in triglycerides concentration was the only statistically significant change observed in the serum of starved

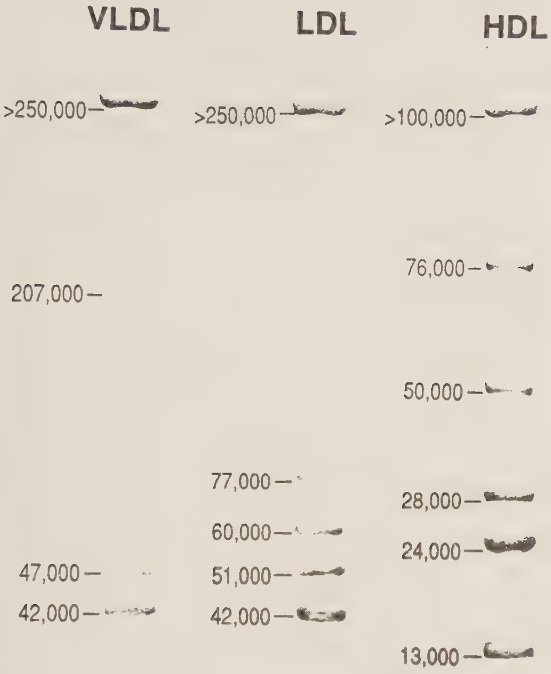

FIG. 1. Representations of sodium dodecyl sulphate-polyacrylamide gels of striped bass apolipoproteins. Apo-VLDL and apo-LDL were electrophoresed in 5% monomer gels and apo-HDL in 10.5% monomer gels. Gels were stained with Coomassie Briliant Blue and molecular weights were calculated from a series of molecular weight protein standards.

striped bass. This decline was not unexpected, however, since it is known that during the initial phases of starvation in fish triglycerides are catabolized while other lipids remain largely unchanged (Love 1980). Also, it has been shown in pink salmon (*Oncorhynchus gorbuscha*) that, during the nonfeeding spawning migration, the liver's triglyceride synthetic ability is lost and blood triglyceride levels fall (Phleger 1971). Decreased serum or plasma triglycerides have been observed in (*Oncorhynchus mykiss* (formerly *Salmo gairdnerii*; Takashima et al. 1971), *Salmo alpinus* (Dannevig and Norum 1983), and *Pleuronectes platessa* (White and Fletcher 1986) after periods of starvation.

Serum Lipoproteins

All the major lipid components were found to a variable extent in each serum lipoprotein class. Variability in the concentrations of lipid components between fish within each treatment group was high and has been noted in other fish species (Chapman et al. 1977; Fremont et al. 1981; Farrell and Munt 1983).

The lipid and protein composition of lipoprotein classes in the serum of fed striped bass was generally similar to that found in rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981). In comparison with rainbow trout, striped bass VLDL was somewhat richer in triglycerides and depleted in cholesterol esters. The LDL of striped bass contained the most total cholesterol (free + esterified) of all the lipoprotein classes; however, triglycerides were the predominant lipid in fed striped bass LDL. Phospholipids accounted for the greatest proportion of striped bass HDL lipid, consistent with other fish species studied (Chapman 1980). Otherwise, the HDL of fed striped bass was composed of similar proportions of triglycerides and cholesterol, lower cholesterol esters, and greater protein in relation to the composition of HDL in salmonids (Nelson and Shore 1974; Chapman et al. 1978; Skinner and Rogie 1978; Fremont et al. 1981).

The apoproteins of striped bass lipoprotein classes were characterized only by their molecular weights. This technique, by itself, does not constitute definite identity but is often used for comparative purposes between lipoprotein classes or with data from other species. In the SDS-PAGE of striped bass VLDL and LDL, the apoprotein band with a molecular weight >250 000 daltons was by far the largest and most intensely stained and may be analogous to mammalian apo-B (Eisenberg 1979; Steinberg 1979). Electrophoretic separations of VLDL and LDL from other fish species have found a similar apoprotein which, in combination with immunological and chemical analyses, has been determined to resemble apo-B (Mills et al. 1977; Chapman et al. 1978). Striped bass VLDL and LDL contained several other apoproteins of lower molecular weights in lesser amounts. This was also the case with rainbow trout (Chapman et al. 1978; Skinner and Rogie 1978). The HDL of striped bass differed from VLDL and LDL in that the primary apoproteins had molecular weights of about 24 000 and 13 000 daltons, and based on these weights may be similar to human apo-AI (27 000 daltons) and apo-AII (17 000 daltons) (Schaefer and Levy 1979). Rainbow trout HDL was found to contain predominantly apoproteins characteristic of apo-AI and apo-AII (Chapman et al. 1978; Skinner and Rogie 1978). The results of the present study and those from studies of fish, birds (Chapman et al. 1977), and mammals (Hollanders et al. 1986) would suggest that the apolipoprotein composition of higher vertebrates is generally similar.

The concentration of total serum lipoproteins in both fed and starved striped bass was high, on the order of that found in salmonids (Nelson and Shore 1974; Chapman et al. 1978; Skinner and Rogie 1978), and reflects the importance of lipids in fish metabolism. Although the total serum lipoprotein concentration was unchanged by starvation, the relative contribution of lipoprotein classes was affected such that VLDL declined and HDL increased. Further, the changes in lipid distributions within serum lipoprotein classes of starved striped bass indicate that there were greater adjustments of lipid metabolism and transport produced by starvation than would be evident by simply assessing lipid changes in serum.

The largest change, on a mean weight percent basis, in the VLDL and LDL of starved striped bass was the depletion of triglycerides. Since VLDL is the principal transport vehicle for triglycerides (Eisenberg 1979) and LDL is formed from VLDL (Brown and Goldstein 1986), it may be expected that the combined influences of no ingestion, depletion of body reserves, and reduced triglyceride synthesis would result in decreased VLDL and LDL triglycerides.

In starved striped bass, HDL composition was the least affected of the serum lipoproteins. The HDL have been shown to be involved in "reverse" cholesterol transport, from peripheral tissues back to hepatocytes (Miller et al. 1985), and cholesterol and phospholipid exchanges between lipoproteins and tissues (Glomset 1979). Cholesterol and cholesterol ester values were unaffected by starvation in striped bass HDL, both in mean weight percent and concentration. These results are similar to those of Black and Skinner (1986), using cholesterol concentration as an estimator of lipoprotein concentrations in rainbow trout. They found that 8 wk starvation produced no change in HDL cholesterol but diminished VLDL and LDL levels.

Phospholipids in the HDL of starved striped bass remained the same as in the HDL of fed fish on a weight percent basis, but the concentration increased significantly ($P<0.001$). The increased concentration of phospholipids, along with protein, was responsible for the increased HDL in starved striped bass compared with fed. In fact, phospholipids in HDL of starved striped bass accounted for 78% of the total serum phospholipid concentration, whereas phospholipid in fed fish HDL comprised about 50% of total serum levels.

Fish biomembranes contain 25 to 80 percent lipid, mainly phospholipids which are characteristically enriched in polyunsaturated fatty acids (PUFA), primarily $22{:}6(n-3)$ (Henderson and Tocher 1987). The $22{:}6(n-3)$ PUFA is an essential fatty acid in most fish species and is critical to growth and maintaining membrane fluidity in colder environments (Sargent et al. 1989). Striped bass are known to require $22{:}6(n-3)$ for growth and membrane synthesis, and tissue levels of this essential fatty acid were selectively maintained during starvation (Martin et al. 1984). The results of the present study indicate that HDL assumes increased importance in the transport of phospholipids containing essential PUFA for maintenance of tissue integrity during starvation, and perhaps for the synthesis of gonadal tissue during annual reproductive development. The increased role of HDL during reproductive development has been suggested from the results of previous work on salmonids by Nelson and Shore (1974) and Fremont and Marion (1982). High levels of HDL were found in the serum of pink salmon (*Oncorhynchus gorbuscha*) just prior to spawning and after weeks to months of starvation; VLDL and LDL were undetected (Nelson and Shore 1974) but were evident in the early prespawning phase. In this study, phospholipid was about 50% of the lipid in HDL and contained $22{:}6(n-3)$ and $20{:}5(n-3)$ as the predominant PUFAs. Fremont and Marion (1982) found similar results in spermiating rainbow trout, where HDL accounted for greater than 50% of the serum lipoproteins with phospholipid comprising 70% of the lipid in HDL. Additionally, $22{:}6(n-3)$ was the predominant PUFA in the phospholipids. Since phospholipids, enriched in $22{:}6(n-3)$, predominate in egg yolk lipids of striped bass (Eldridge et al. 1983), it is reasonable that HDL functions as a primary vehicle for the transport of structural lipids and essential PUFA for gonadal maturation during the nonfeeding spawning period.

The findings of high serum levels of lipoproteins, and particularly HDL, in striped bass during starvation indicate their important role in permitting fish to withstand long periods without food by distributing lipids to tissues in order to maintain their integrity, whether or not starvation is accompanied by gonadal development. Furthermore, HDL appears to assume greater significance in facilitating the transport of structural lipids and essential PUFA during periods of starvation.

References

Black, D., and E. R. Skinner. 1986. Features of the lipid transport system of fish as demonstrated by studies on starvation in the rainbow trout. J. Comp. Physiol. B 156: 497–502.

Brown, M. S., and J. L. Goldstein. 1986. A receptor-mediated pathway for cholesterol homeostasis. Science (Wash., DC) 232: 34–47.

Bucolo, G., and H. David. 1973. Quantitative determinations of serum triglycerides by the use of enzymes. Clin. Chem. 19: 476–482.

Chapman, M. J. 1980. Animal lipoproteins: chemistry, structure, and comparative aspects. J. Lipid Res. 21: 789–853.

Chapman, M. J., S. Goldstein, G. L. Mills, L. Fremont, and C. Leger. 1977. Some aspects of the serum lipoproteins in the rainbow trout. Protides Biol. Fluid, Proc. Colloq. 25: 487–490.

Chapman, M. J., S. Goldstein, G. L. Mills, and C. Leger. 1978. Distribution and characterization of the serum lipoproteins and their apoproteins in the rainbow trout (*Salmo gairdnerii*). Biochem. 17: 4455–4464.

Chapman, M. J., G. L. Mills, and J. H. Ledford. 1975. The distribution and partial characterization of the serum apoliproteins in the Guineapig. Biochem. J. 149: 423–436.

Cowey, C. B., and J. R. Sargent. 1979. Nutrition, p. 1–70. *In* W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. VIII. Bioenergetics and growth. Academic Press, New York, NY.

Dannevig, B. H., and K. R. Norum. 1983. Effects of fasting on plasma lipids and cholesterol esterification in plasma, liver and intestinal mucosa in the char (*Salmo alpinus* L.). Comp. Biochem. Physiol. 74B: 243–250.

Eisenberg, S. 1979. Very-low-density lipoprotein metabolism, p. 139–165. *In* S. Eisenberg [ed.] Progress in biochemical pharmacology. Vol. 15. Lipoprotein metabolism. S. Karger, Basel, Switzerland.

Eldrige, M. B., J. D. Joseph, K. M. Taberski, and G. T. Seaborn. 1983. Lipid and fatty acid composition of the endogenous energy sources of striped bass (*Morone saxatilis*) eggs. Lipids 18: 510–513.

Farrell, A. P., and B. Munt. 1983. Cholesterol levels in the blood of Atlantic salmonids. Comp. Biochem. Physiol. 75A: 239–242.

Fremont, L., C. Leger, and M. Boudon. 1981. Fatty acid composition of lipids in the trout — II. Fractionation and analysis of plasma lipoproteins. Comp. Biochem. Physiol. 69B: 107–113.

Fremont, L., and D. Marion. 1982. A comparison of the lipoprotein profiles in male trout (*Salmo gairdneri*) before maturity and during spermiation. Comp. Biochem. Physiol. 73B: 849–855.

Glomset, J. A. 1979. Lecithin:cholesterol acyltransferase. An exercise in comparative biology, p. 41–66. *In* S. Eisenberg [ed.] Progress in biochemical pharmacology. Vol. 15. Lipoprotein metabolism. S. Karger, Basel, Switzerland.

Harvey, H. R., and J. S. Patton. 1981. Solvent focusing for the rapid and sensitive quantification of total lipids on Chromarods. Anal. Biochem. 116: 312–316.

Henderson, R. J., and D. R. Tocher. 1987. The lipid composition and biochemistry of freshwater fish. Prog. Lipid Res. 26: 281–347.

Herbert, P. N., L. L. Bausserman, L. O. Henderson, R. J. Heinen, M. J. LaPiana, E. C. Church, and R. S. Shulman. 1978. Apolipoprotein quantitation, p. 35–56. *In* H. Peeters [ed.[The lipoprotein molecule. Plenum Press, New York, NY.

Hollanders, B., A. Mougin, F. N'Diaye, E. Hentz, X. Aude, and A. Girard. 1986. Comparison of the lipoprotein profiles obtained from rat, bovine, horse, dog, rabbit and pig serum by a new two-step ultracentrifugal gradient procedure. Comp. Biochem. Physiol. 84B: 83–89.

Jones, P. L., and B. D. Sidell. 1982. Metabolic responses of striped bass (*Morone saxatilis*) to temperature acclimation. II. Alterations in metabolic carbon sources and distributions of fiber types in locomotory muscle. J. Exp. Zool. 219: 163–171.

Kayama, M. 1975. Studies on the lipids of micronektonic fishes caught in Sagami and Suruga Bays, with special reference to their wax esters. J. Japan Oil Chem. Soc. (Yukagaka) 24: 435–440.

Laemmli, U. K. 1970. Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature (Lond.) 227: 680–685.

Lindgren, F. T. 1975. Preparative ultracentrifugal laboratory procedures and suggestions for lipoprotein analysis, p. 204–224. *In* E. G. Perkins [ed.] Analysis of lipids and lipoproteins. American Oil Chemist's Society, Champaign, IL.

Love, R. M. 1970. The chemical biology of fishes. Academic Press, New York, NY. 547 p.

1980. The chemical biology of fishes. Vol. 2. Advances 1968–1977. Academic Press, New York, NY. 943 p.

Markwell, M. A. K., S. M. Haas, N. E. Tolbert, and L. L. Bieber. 1981. Protein determination in membrane and lipoprotein samples: manual and automated procedures, p. 296–303. *In* J. M. Lowenstein [ed.] Methods in enzymology. Vol. 72. Lipids, Part D. Academic Press, New York, NY.

Martin, F. D., D. A. Wright, and J. C. Means. 1984. Fatty acids and starvation in larval striped bass (*Morone saxatilis*). Comp. Biochem. Physiol. 77B: 785–790.

Miller, N. E., A. La Ville, and D. Crook. 1985. Direct evidence that reverse cholesterol transport is mediated by high-density lipoprotein in rabbits. Nature (Lond.) 314: 109–111.

Mills, G. L., and C. E. Taylaur. 1977. Comparative studies of fish low density lipoproteins. Protides Biol. Fluid, Proc. Colloq. 25: 477–482.

Mills, G. L., C. E. Taylaur, M. J. Chapman, and G. R. Forster. 1977. Characterization of serum lipoproteins of the shark *Centrophorus squamosus*. Biochem. J. 163: 455–465.

Mori, M., S. Hikichi, H. Kamiya, and Y. Hashimoto. 1972. Three species of teleost fish having diacyl glyceryl ethers in the muscle as a major lipid. Bull. Jap. Soc. Scient. Fish. 38: 56–63.

Nelson, G. J., and V. G. Shore. 1974. Characterization of the serum high density lipoproteins and apolipoproteins of pink salmon. J. Biol. Chem. 249: 536–542.

Phleger, C. F. 1971. Liver triglyceride synthesis failure in post-spawning salmon. Lipids 6: 347–349.

Sargent, J., R. J. Henderson, and D. R. Tocher. 1989. The lipids, p. 153–218. *In* J. E. Halver [ed.] Fish nutrition. 2nd ed. Academic Press, San Diego, CA.

Schaefer, E. J., and R. I. Levy. 1979. Composition and metabolism of high-density lipoproteins, p. 200–215. *In* S. Eisenberg [ed.] Progress in biochemical pharmacology. Vol. 15. Lipoprotein metabolism. S. Karger, Basel, Switzerland.

Shul'man, G. E. 1972. Life cycles of fish. Physiology and biochemistry. 258 p. Moscow. (Transl. from Russian by N. Kaner and H. Hardin 1974). John Wiley and Sons, New York, NY.

Skinner, E. R., and A. Rogie. 1978. The isolation and partial characterization of the serum lipoproteins and apolipoproteins of the rainbow trout. Biochem. J. 173: 507–520.

Steinberg, D. 1979. Origin, turnover and fate of plasma low-density lipoproteins, p. 166–199. *In* S. Eisenberg [ed.] Progress in biochemical pharmacology. Vol. 15. Lipoprotein metabolism. S. Karger, Basel, Switzerland.

Stevens, D. E. 1966. Food habits of striped bass, *Roccus saxatilis*, in the Sacramento-Jan Joaquin delta, p. 68–96. *In* J. L. Turner and D. W. Kelley [ed.] Ecological studies of the Sacramento-San Joaquin delta. Part II. Fishes of the delta. Calif. Dept. Fish Game, Fish. Bull. 136. Sacramento, CA.

Takashima, F., T. Hibiya, T. Watanabe, and T. Hara. 1971. Endocrinological studies on lipid metabolism in rainbow trout — I. Differences in lipid content of plasma, liver and visceral adipose tissue between sexually immature and mature females. Bull. Jap. Soc. Scient. Fish. 37: 307–311.

Weber, K., and M. Osborn. 1969. The reliability of molecular weight determinations by dodecyl sulfate-polyacrylamide gel electrophoresis. J. Biol. Chem. 244: 4406–4411.

White, A., and T. C. Fletcher. 1986. Serum cortisol, glucose and lipids in plaice (*Pleuronectes platessa* L.) exposed to starvation and aquarium stress. Comp. Biochem. Physiol. 84A: 649–653.

Woodhull, C. 1947. Spawning habits of the striped bass (*Roccus saxatilis*) in California waters. Calif. Fish Game 33: 97–102.

Presence-Absence Sampling for Fisheries Management[1]

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It is often important to estimate the abundance of a fish stock when the stock is somewhat depleted. For pelagic species this presents great operational difficulties, because adult surveys may be prohibitively expensive and time consuming. Here we introduce a method for estimating the spawning biomass of a stock by means of egg or larval surveys. In particular, we develop a series of models for presence-absence sampling of eggs or larvae and show how presence-absence data can be used to estimate adult spawning biomass. The models are based on an underlying probabilistic description of the aggregation of eggs or larvae, a search process, and a description of habitat structure. Methodologies are given for estimating the distribution of the size of the spawning biomass from presence-absence data. A case study of sardine is used to justify a number of the assumptions. The methods are applied to a 1985 survey for sardine eggs and are compared to an alternative method based on egg production.

Dans bon nombre de cas, il est important d'estimer l'abondance d'un stock de poissons lorsque ses effectifs sont quelque peu réduits. Pour les espèces pélagiques, cela entraîne des difficultés opérationnelles majeures, car le dénombrement des adultes peut être excessivement coûteux et long. Les auteurs ont mis au point une méthode permettant d'estimer la biomasse des géniteurs d'un stock par la présence ou l'absence de leurs oeufs ou de leurs larves. À cette fin, ils ont élaboré une série de modèles et démontrent comment l'on peut se servir de données relatives à la présence ou à l'absence des oeufs ou des larves de poisson pour estimer la biomasse des géniteurs adultes. Les modèles reposent sur un calcul probabiliste du rassemblement des oeufs ou des larves, une méthode de recherche et une description de la structure de l'habitat. Les auteurs donnent des techniques pour estimer la répartition de la biomasse des géniteurs d'après les données sur la présence et l'absence des oeufs ou des larves. Ils ont recours à une étude relative aux sardines pour justifier un certain nombre d'hypothèses. Ils appliquent leurs méthodes à une étude au sujet d'oeufs de sardine datant de 1985, et les comparent à une autre méthode d'estimation reposant sur la production d'oeufs.

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Very often, fisheries managers must estimate the adult biomass of pelagic stocks. When the stocks are depleted, direct assessment of adult population levels is not only difficult, but may be highly inaccurate (Hewitt et al. 1984). In such situations, an alternative is the survey of egg or larval populations as a means of estimating adult biomass (Lasker 1981). The interpretation of data from egg or larval surveys, called plankton surveys in this paper, is complicated by the patchy and highly aggregated nature of eggs and larvae (Smith 1978). A method based on egg production (Santander et al. 1982; Hewitt 1984; Hewitt et al. 1984; Lasker 1985; Wolf and Smith 1985; Wolf et al. 1987) has been proposed as a means of relating the data from egg surveys to adult biomass. The objective of this paper is to introduce another set of tools which can be used by the fisheries scientist or manager who is involved in egg or larval surveys.

The work reported here was motivated by the need to manage the recovery of the northern population of California sardine, *Sardinops sagax caerulus* (Wolf 1986). Once a thriving population, with a peak standing biomass estimated to be 11×10^6 metric tons (t) in the California current in 1860, to about 4×10^6 t during the cannery heyday (Smith 1978), it is no longer strong. Current State law (Wolf 1986) prohibits any direct fishery on sardine (there will always be incidental catch that is essentially uncontrollable) until the spawning biomass (the fraction of standing biomass older than 2 yr) exceeds 20 000 short tons (1 short ton = 0.907 t). If the spawning biomass is determined to exceed the critical level of 20 000 short tons, then a fishery with a catch quota of about 5% of the spawning biomass is recommended.

The methodology developed here, however, should be applicable to a wide variety of other plankton sampling programs (e.g. Sette and Ahlstrom 1948; Squire 1983) and many benthic sampling programs (Downing 1979; Resh 1979). The methodology introduced here addresses the same kinds of problems as the work of Pennington (1983) but does so with very different techniques.

For the current management of sardine, the key question is whether the biomass exceeds a critical level B_c (in this case 20 000 short tons). We thus do not need to estimate the mean and variance of the spawning biomass directly, but instead want to assess the probability that the biomass exceeds the critical level. We do this as follows: first, we associate the critical level of biomass B_c with a critical level m_c of eggs per sampling station. Second, given the sampling data, we estimate the probability that the mean of the distribution of eggs per sampling station exceeds m_c.

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[1] Dedicated to the memory of Reuben Lasker, an exemplary scientist and individual.

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In the next section, the models for egg and larval distributions are developed and discussed. In the third section, a sequence of sampling models is developed. Particular attention is paid to the justification for presence–absence sampling (PAS). In the fourth section, the methodology developed here is compared with a method based on egg production. We then develop a criterion indicating when direct counts are preferable to presence–absence sampling. A case study of sardine from 1940–65 is used to justify a number of the assumptions necessary for the analysis. We conclude with a discussion illustrating how presence–absence sampling can be placed into the overall context of management.

Models for Egg and Larval Distribution

Eggs and larvae are commonly distributed over space in an aggregated and patchy manner. Although this aggregation is undoubtedly behavioral in nature (Vlymen 1977; Lasker 1981; Grosberg and Quinn 1986), the models introduced here are operational ones, with attempted biological justification. The highly aggregated nature of eggs and larvae means that samples of egg counts will have considerable dispersion. That is, a high proportion of the samples will have no eggs and samples that have one egg are likely to have many. A typical situation is the following data on anchovy eggs: for a survey involving 419 samples there were 208 samples with no eggs; the range for positive samples was 2–12 200 eggs per sample. The mean was 206 eggs/sample and the SD was 1022 (i.e. a coefficient of variation of about 500%). Compared to sardine, anchovy is a healthy stock, leading to many samples with eggs. For example, in the 1985 sardine cruise discussed in the fourth section, only 11 of 419 sites sampled had eggs. The actual counts of eggs per positive station were 42, 15, 10, 5, 5, 5, 3, 2, 1, 1, 1; these data have mean 7.8 and SD 11.6 for a coefficient of variation about 150%.

Some of the samples with no eggs occur because samples are taken beyond the current habitat of the population. That is, if we knew exactly the current range of the population, it would be possible to design surveys in which a much higher proportion of samples had eggs. The difficulty for pelagic species is that the spatial range of habitat can vary considerably (see, e.g. Lasker 1985, p. 18); thus the sampling must both determine the boundaries of the habitat and estimate abundance. We believe that in some cases, fully ⅔ of the samples may be used to define the boundary of the current range of the spawning population. That is, in some cases more than 50% of the samples taken may have no eggs and will be used to help delineate the boundaries of the habitat. A good, operational model should be compatible with the assumptions that (1) not all samples will be in the habitat of the spawning stock, (2) samples in the habitat may still show high levels of aggregation.

The question of spatial scale is an important one as well. For the sardines, the relevant spatial scales are:

Unit	Spatial scale
Individual fish	~ cm
School	~ 100 m
Egg patches	~ 1000 m
School groups	~ 10 000 m
Sampling scale	~ 10 000 m

The actual area of the device used to sample sites in the ocean is 0.05 m^2. It is reasonable then to assume that samples taken at different sites (called stations) are independent random variables. Let (Table 1 summarizes symbols and their interpretations)

(1) X_i = number of eggs (or larvae) taken at the i^{th} station.

The properties of X_i suggested by the empirical data are

(i) $X_i \geqslant 0$,
(ii) $Pr\{X_i = 0\}$ is considerable, and
(2) (iii) $\text{Var}\,\{X_i\} >> E\,\{X_i\}$.

In this equation, Var{ } and E{ } denote the variance and mean of a random variable respectively, and $Pr\{X=x\}$ is the probability that the random variable X takes the value x. The variance greatly exceeding the mean is a commonly accepted definition of an overdispersed or aggregated population.

One model with properties (i)–(iii) is the negative binomial (*NB*) distribution. At the outset, we stress that using the *NB* is not crucial to any of the conceptual development that follows. We choose it because it is commonly used in ecological modeling. We will show below that other distributions could be used as well. For the *NB* distribution,

$$\begin{aligned} & Pr\{X_i = x \mid \text{station is a habitat}\} \\ (3)\quad & = [\Gamma(k+x)/\Gamma(k)x!]\ [k/k+m]^k\ [m/k+m]^x \end{aligned}$$

In this equation, $\Gamma(x)$ is the gamma function, and k and m are parameters. In particular,

$$(4)\quad Pr\{X_i = 0 \mid \text{station is a habitat}\} = [k/k+m]^k$$

The conditional mean and variance of X_i are (Johnson and Kotz 1969)

$$\begin{aligned} & E\{X_i \mid \text{station is a habitat}\} = m \\ (5)\quad & \text{Var}\{X_i \mid \text{station is a habitat}\} = m + m^2/k \end{aligned}$$

so that m is the mean of the distribution and k is a measure of the amount of "overdispersion" relative to the Poisson distribution.

Often k is essentially independent of spawning biomass, although it depends upon sampling scale (DeBouzie and Thioulouse 1986). Smith and Richardson (1977, p. 57) found, for example, that for sardine eggs the estimate of k varied between 0.08 and 0.21 as the spawning biomass varied between 0.2 and 3.9 × 10^6 t. This is a variation of less than a factor of 3 in k, during variation by a factor of 19.5 in biomass; we interpret this as relative constancy of k.

The value of k may also be tied to the life history of the species (Hewitt 1981). Table 2 shows our estimate of the life history dependence of k for the early stages of anchovy (P. E. Smith, unpubl. data). Because of the depleted nature of sardine, we are unable to determine a similar life history dependence of k at the present time.

The *NB* model has a long and distinguished history in ecology (e.g. Anscombe 1948, 1950; Taylor 1953; Sampford 1956; Bliss and Owen 1958; Bissell 1972; Pielou 1977; Taylor et al. 1979; Ripley 1981; Zweifel and Smith 1981; Diggle 1983; Dennis and Patil 1984). It also has limitations. For example, L. R. Taylor and his colleagues (Taylor et al. 1979; Perry and Taylor 1986) have sharply attacked the use of the *NB* distribution with

TABLE 1. Summary of symbols, interpretations, and values for computations.

Symbol	Interpretation	Value used and source
B, B_c	Spawning biomass and its critical level	20 000 short tons (State of California Law)
X_i	Number of eggs at the i^{th} station	Random variable
m	Mean number of eggs at a station	Estimated by the procedure
k	Overdispersion parameter of negative binomial distribution	Ranges from 0.08 to 0.21 for sardine eggs (Smith and Richardson, 1977)
p_i	Probability that the i^{th} station is a habitat for the spawning stock	All $p_i = p = 0.05$(historical data)
m_c	Critical value of m, linearly related to critical value of biomass	$m_c = 1.14$ (historical data)
Y_i	Number of eggs detected at the i^{th} station	Random variable
α_i	Maximum probability of detecting eggs at the i^{th} station when eggs are overly abundant	$\alpha_i = 1$
b_i	Sampler efficiency	Varies between 1/6 and 6
$\mathcal{P}$, $\mathcal{N}$	Denote samples with positive number of eggs and no eggs	Data
$\mathcal{L}$	Likelihood of an egg sample	Computed by Eq. (12)
$\hat{m}$	Maximum likelihood estimator (MLE) for m	Computed by methods of this paper
N_n, N_p, N	Number of samples with no eggs or a positive number of eggs, respectively and total number of samples	Data; $N = N_n + N_p$
$R(m, \hat{m})$	Likelihood ratio of a value of m relative to MLE	Computed by Eq. (16)
Y_{ij}	Presence or absence of eggs of age group j at station i	Data
k_j, m_j	Overdispersion parameter and mean number of eggs of age group j	Age dependence given by Smith (1973)
$r_c(i)$	Association or correlation coefficient for the presence of eggs of different age groups at station i	Varies between 0 and 1.

TABLE 2. Early life history values of the negative binomial k for northern anchovy larvae (P. E. Smith, unpubl. data).

Length (mm)	Value of k	
	Day	Night
3.25	0.064	0.073
5.25	0.093	0.104
7.25	0.102	0.121
9.25	0.095	0.126
11.25	0.069	0.120
13.25	0.038	0.085
15.25	0.019	0.053
17.25	0.006	0.036

constant k. They propose that k is always a function $k(m)$ of the mean and that one should use Taylor's power law (Variance = $a \cdot m^b$, where a and b are constants) and a moment estimator for the variance to determine the form of the function $k(m)$. It is our opinion that, for egg sampling especially, k can be treated as constant. That is, we believe that eggs are highly clumped in order to insure successful fertilization and thus the clumping should be relatively independent of spawning biomass. Mangel (1987) discusses other biological motivations for choosing the *NB* distribution.

The distribution given in Eq. (3) is conditioned on the assumption that the i^{th} station is a habitat for the spawners. Let

$$(6) \quad p_i(m) = Pr\{\text{the } i^{th} \text{ station is a habitat for the spawners}\}$$

Methods for determining the functional form of $p_i(m)$ will be described in the next section. We assume that p_i may depend upon m because as the stock abundance increases and decreases, the spawning habitat used by the stock may expand and contract (MacCall 1988). Since m increases with biomass, the net effect is that the probability that a station is a habitat for the spawners depends upon biomass, and through that, m. Note, however, that we do not assume that all samples are taken at stations that are habitats.

The unconditional distribution of eggs at stations is then

$$Pr\{X_i = 0\} = Pr\{\text{station is not a habitat}\} + Pr\{\text{station is a habitat and no eggs are present}\}$$
$$= (1-p_i(m)) + p_i(m)\,[k/k+m]^k$$

$$Pr\{X_i>0\} = 1 - Pr\{X_i=0\}$$
$$= p_i(m)\{1 - [k/k+m]^k\}$$

$$Pr\{X_i = x>0\} = Pr\{\text{station is a habitat and } x \text{ eggs are present}\}$$

$$(7) \quad = p_i(m)\,\{[\Gamma(k+x)/\,\Gamma(k)x!]\,[k/k+m]^k\,[m/k+m]^x\}.$$

In the analysis that follows, we assume that k is known but that m is unknown and that the objective of the sampling is to make inferences about m. In particular, we assume that the adult biomass and mean number of eggs per station are linearly related. In general, this assumption must be verified by historical data, which we do in the case study. This means that there is a critical value of m, denoted by m_c, related to the critical level of biomass B_c in the sense that

$$(8) \quad Pr\{B>B_c\} = Pr\{m>m_c\}.$$

In order to justify this assumption, we must either back-calculate from egg abundance to spawning biomass level (e.g. Lasker 1985; Wolf and Smith 1985, 1986) or use historical data that relate previous levels of spawning biomass and mean egg density to determine the value of m_c, as in the case study presented below.

Other types of ''contagious'' distributions can be used in the analysis in place of the *NB* distribution. Some choices are discussed in the Appendix.

Presence–Absence Sampling

In this section, presence–absence sampling (PAS) is described as a method for estimating and making inferences about m. A number of extensions of the basic *NB* model — including imperfect detection of the plankton and multiple age groups — are described.

In presence–absence sampling, the incidence of eggs over space (time is essentially ''fixed'' over a short interval) is determined and used to estimate the spawning biomass. There are a number of reasons, both analytical and operational, for simply noting the incidence of eggs rather than counting them. First, for certain distinctive eggs (e.g. northern anchovy), PAS can be done on board ship whereas counting eggs requires extensive off ship effort. (In order to reduce possible errors in on-ship presence–absence sampling, one often introduces a threshold [e.g. 4 or 5 eggs]: a sample is marked as ''eggs present'' only if the number of observed eggs exceeds the threshold.) Thus, PAS could be done as a ''real time'' operation. Second, when the overdispersion parameter k is small (e.g. $k < 0.1$), the eggs or larvae will be highly aggregated and thus estimating the value of m with any precision from a sample mean will require a large number of samples, usually larger than the number available. In addition, the value of the sample mean will often be driven by one or two large samples; sampling for incidence avoids this problem. (As the spawning biomass increases, however, so that virtually all stations have eggs, one should switch from PAS to actual counts. Below, we describe a way to determine when the switch should be made). For problems in which one needs to determine habitat boundaries as well as spawning biomass it is likely that most stations will have no eggs. (As behavioral information about the species, and the effects of physical variables becomes better known, it may be possible to reduce the number of stations without eggs by satellite presurvey or appropriate design of the survey.) Smith (1973) discusses how overdispersal may affect estimates of survival.

We extend Eq. (7) to include the failure to detect eggs present at a site. Let Y_i denote the number of eggs in the sample at the i^{th} station. There are three ways to obtain $Y_i = 0$: (1) the station is not a habitat for the spawning species; (2) the station is a habitat and there are no eggs present; and (3) the station is a habitat, there are eggs present, but the sampler misses the eggs. The models developed thus far account for (1) and (2) but not for (3), which is a likely possibility since the CalCOFI stations (Fig. 1) represent about 102 km^2 and the sampler area is 0.05 m^2. Introduce a detection function

$$(9) \quad Pr\,\{\text{detect eggs} \mid \text{number of eggs present } X_i = x\}$$
$$= \alpha_i\,(1 - e^{-b_i x})$$

where $0 \leqslant \alpha_i \leqslant 1$ is the maximum probability of detecting eggs as $X_i \rightarrow \infty$ and b_i is a measure of sampler efficiency when eggs are present. Eq. (9) represents a random search formula (Mangel 1985a, b, 1987). We thus obtain

$$Pr\{Y_i=0\}$$
$$= Pr\{\text{station is not a habitat}\} + Pr\{\text{station is a habitat}\}\,\Sigma_x\,Pr\{x \text{ eggs present}\}Pr\{\text{no detection at the level } x\}$$
$$= (1 - p_i) +$$
$$(10) \quad p_i\Sigma_x\,[\Gamma(k+x)/\Gamma(k)x!]\,[k/k+m]^k[m/k+m]^x\,\{1 - \alpha_i(1-e^{-b_i x})\}$$

Eq. (10) can be simplified by the use of the moment generating function for the *NB* distribution and becomes

$$(11) \quad Pr\{Y_i = 0\} = (1 - \alpha_i p_i) + \alpha_i p_i\,[k/(k+m(1-e^{-b_i}))]^k$$

Eq. (11) is the sarting point for the rest of the analysis in this paper.

To recap: we want to estimate m from values of Y_i and assume that the parameters α_i, p_i, b_i, and k are known. The first three are essentially operational parameters, fixed by the operational situation and equipment. The last, k, is a biological and operational parameter, fixed by the species and the scale of the sampling procedure. The objective is to sample N stations for the incidence of eggs and to then make inferences about the properties of the mean m. In this paper, a Maximum Likelihood Estimation (MLE) approach is adopted (see Edwards 1972 for general discussion); Mangel (1987) discusses Bayesian methods for presence–absence sampling.

Assume that a total of N stations are sampled and that there are N_p stations (indexed by $i \in \mathcal{P}$) at which eggs are discovered and N_n stations (indexed by $j \in \mathcal{N}$) at which no eggs are discovered. The likelihood $\mathcal{L}$ of such a data set is constructed from the basic model Eq. (11). Begin by setting

$$(12) \quad w_i = 1 - e^{-b_i}$$

The likelihood of the data set is then

$$(13) \quad \mathcal{L} = \Pi_{j\in\mathcal{N}}\,[(1 - \alpha_j p_j + \alpha_j p_j\,\{k/(k + mw_j)\}^k]\,\Pi_{i\in\mathcal{P}}\,[\alpha_i p_i - \alpha_i p_i\{k/(k+mw_i)\}^k]$$

From this likelihood function, we want to compute the maximum likelihood estimate (MLE) for m. The MLE, which we denote by $\hat{m}$, must generally be computed numerically. There

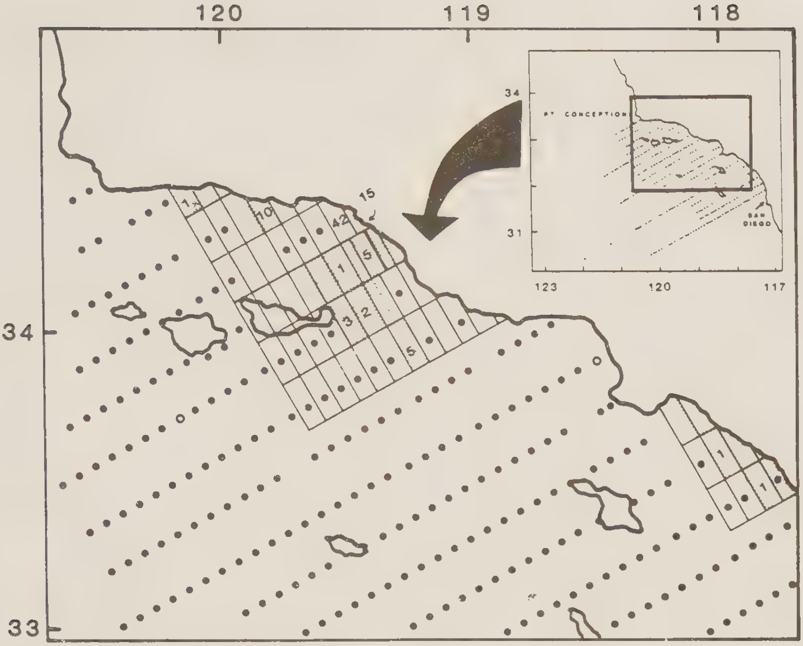

FIG. 1. Sampling stations with eggs in the May, 1985 sardine survey.

is at least one case, however, in which $\hat{m}$ can be found analytically. This is the special case in which for all values of i $p_i = p$, $\alpha_i = \alpha$, and $w_i = w$. This assumption must be somewhat restrictive, since it is based on the assumption of uniformity of oceanic habitat over space. On the other hand, for a survey done over a relatively small region and done quickly, these assumptions might be valid. Assuming the constancy of α, p, and w, leads to the likelihood

$$(14)\quad \mathscr{L} = [1 - \alpha p + \alpha p\{k/(k+mw)\}^k]^{N_n} \times [\alpha p - \alpha p\{k/(k+mw)\}^k]^{N_p}.$$

In this equation, N_n and N_p are the number of stations with no eggs and with eggs, respectively. Set $N = N_n + N_p$, so that N is the total number of stations sampled. Direct computation shows that the MLE is

$$(15)\quad \hat{m} = (k/w)[\{N\alpha p/(N\alpha p - N_p)\}^{(1/k)} - 1]$$

Thus, for fixed k, w, N, and αp, the MLE estimate is a function of the number of positive samples $\hat{m} = \hat{m}(N_p)$. Eq. (15) represents a generalization of a formula due to D. J Gerrard (Southwood 1976, p. 55).

The likelihood can be viewed as a function of m, $\mathscr{L} = \mathscr{L}(m)$ so that the likelihood ratio

$$(16)\quad R(m, \hat{m}) = \mathscr{L}(m)/\mathscr{L}(\hat{m})$$

provides a measure of the relative likelihood of any value of m in comparison to the MLE. Alternatively, $R(m, \hat{m})$ is approximately the posterior distribution of m under Bayesian analysis when a uniform prior is assumed. Figure 2 shows one such likelihood ratio, for parameters corresponding to the 1985 sardine egg cruise shown in Fig. 1. The likelihod ratio is highly skewed with a long tail (indicating the chance, albeit small, of some very large values of m). If m is proportional to the spawning biomass, then we can view $R(m, \hat{m})$ as a likelihood distribution for the biomass. The probability that m exceeds m_c and aproximate confidence intervals for the biomass can then be constructed from this likelihood function (Hudson 1971).

Since the number of positive samples is a random variable, the function $\hat{m}(N_p)$ is also a random variable. Its mean can be computed by the application of Seber's delta method (Seber 1973) and is

$$(17)\quad E\{\hat{m}(N_p)\} \sim \hat{m}(E\{N_p\} + (1/2)\,[\hat{m}''(N_p)\,|_{E\{N_p\}}]\ \mathrm{Var}\{N_p\}$$

where $E\{N_p\}$ is the expected value of N_p and is

$$(18)\quad E\{N_p\} = N\alpha p[1 - \{k/(k+mw)\}^k]$$

and $\hat{m}''(N_p)$ is the second derivative of $\hat{m}(N_p)$; in Eq. (17) it is evaluated at the expected value of N_p.

The following properties are verified

1) $\hat{m}(E\{N_p\}) = m$
2) $\hat{m}''(N_p) =$
$(1/w)\,[(N\alpha p)^{(1/k)}\,(1 + (1/k))\,(N\alpha p - N_p)^{-(2+(1/k))}]$
3) $\mathrm{Var}\{N_p\} = N\alpha p[1 - \{k/(k+mw)\}^k]\,[1 - \alpha p + \alpha p\{k/(k+mw)\}^k]$.

Thus, although we find that $\hat{m}(E\{N_p\}) = m$, it is not in general true that $E\{\hat{m}(N_p)\} = m$ and the MLE is in general a biased estimator. Table 3 provides numerical information on the size of the bias. Note the trend that the bias decreases with decreasing b. The other trend — that the bias decreases with increasing αp — is easily understood since we are dealing with less uncertainty as αp increases.

In order to test the estimation procedures for m further, we used a Monte Carlo simulation to generate data according to

$$(19)\quad Pr\{\text{positive sample}\} = \alpha p[1 - \{k/(k+mw)\}^k]$$

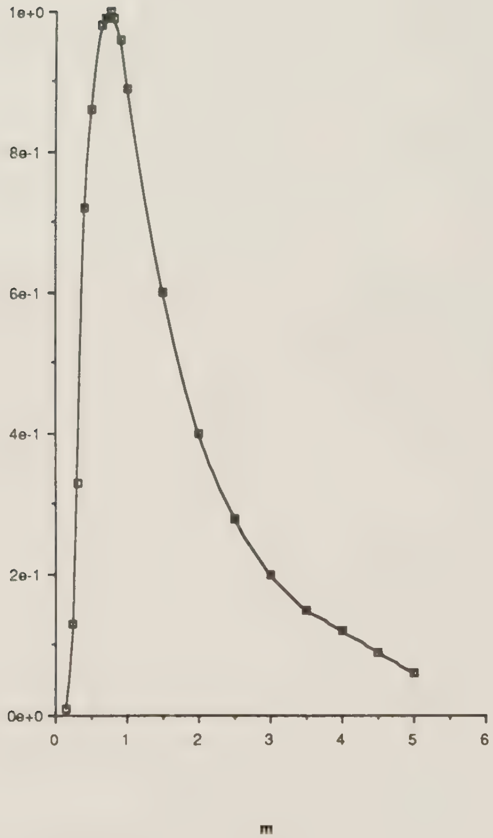

FIG. 2. Likelihood ratio $R(m, \hat{m})$ (Parameters are $\alpha p=0.1$, $b=6$, $k=0.2$, $N=419$, $N_n=408$).

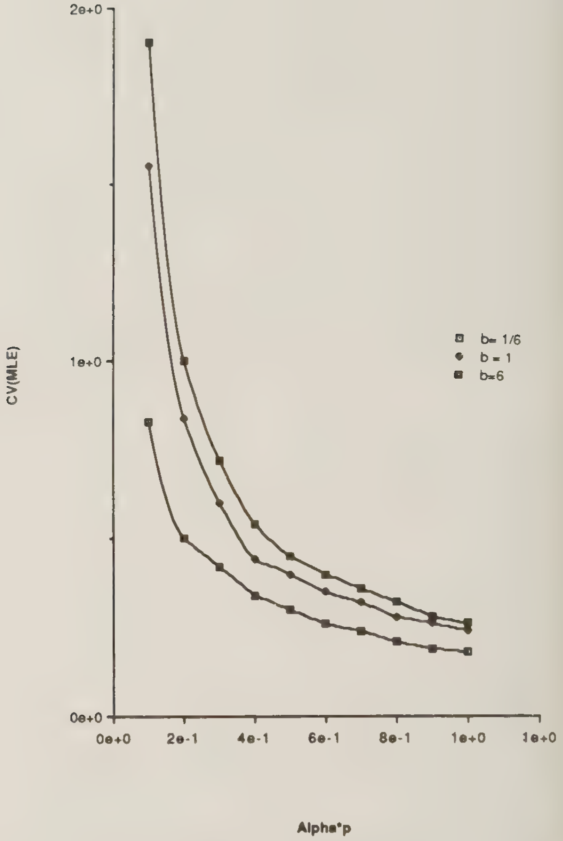

FIG. 3. Coefficient of variation (CV) of the MLE for m, from the simulations, as a function of αp and b. (Parameters are $N=419$, $m=5$, $k=0.2$).

TABLE 3. Bias in the MLE $\hat{m}$ ($N=419$, $m=5$, $k=0.2$).

	Bias for		
αp	$b=6$	$b=1$	b=1/6
1	0.36	0.30	0.18
0.9	0.43	0.36	0.20
0.8	0.53	0.44	0.24
0.7	0.65	0.53	0.28
0.6	0.81	0.66	0.34
0.5	1.04	0.83	0.42
0.4	1.39	1.09	0.54
0.3	1.96	1.54	0.74
0.2	3.10	2.43	1.14
0.1	6.54	5.09	2.34

and in each run of the simulation, the value of $\hat{m}$ was determined. Figure 3 shows the coefficient of variation CV($\hat{m}$) of $\hat{m}$ obtained using the simulations. The same trends with b and αp are observed for the coefficient of variation as for the bias.

In many instances, the eggs or larvae sampled will include different age-classes that involve different levels of dispersion and different means. For example, sardine eggs are usually classified as S (eggs encountered during spawning), A, B, or C (1-, 2-, or 3-d-old). We explicitly extend the model to include age-classes of eggs as follows. Let

$$(20) \quad Y_{ij} = \begin{cases} 1 & \text{if there are eggs of the } j^{\text{th}} \text{ age-group at the } i^{\text{th}} \text{ station} \\ 0 & \text{otherwise.} \end{cases}$$

The natural extension of the basic model is

$$(21) \quad Pr\{Y_{ij} = 0\} = 1 - \alpha_i p_i + \alpha_i p_i \{k_j/(k_j + m_j w_i)\}^{k_j}$$

where k_j and m_j are the values of k and m for the j^{th} age-group. For sardine, we choose the parametrization (Smith 1973; Lasker 1985, p. 17 ff) $k_j = 0.1\,j$ and $m_j = \{1 - 0.3(j-1)\}\,m$ with $j = 1, 2, 3$, or 4 for S, A, B, or C eggs respectively. The interpretation of this parametrization is the following. The k_j increase with time, indicating a more even (less patchy) distribution of older eggs. We presume that this is due to oceanic mixing after spawning. The m_j decrease with time, indicating mortality at about 30% per day for the first 3 d. This 30% per day mortality is true for sardine eggs; for anchovy eggs it is about 20%. Detailed justification of these values, along with variance estimates, is given by Smith (1973) and Smith and Hewitt (1985).

To construct the likelihood function, we now need to include the interaction between eggs of different age-groups. It is conceivable that the presence or absence of eggs of a certain age-group is not completely independent of the presence or absence of eggs of other age-groups. On the other hand, we do not know the exact correlation between eggs or different age-groups. As a way around this difficulty, we introduce a parameter $r_c(i)$ that can be interpreted as a simple "association coefficient" or "presence–absence correlation coefficient": when $r_c(i)$ is set equal to 0, the eggs at the i^{th} station are treated as completely independent, random variables and when $r_c(i)$ is set equal to 1, the eggs at the i^{th} station are treated as completely dependent random variables so that if eggs of one age-class are present, eggs of all age-classes are present. With this model,

$$Pr\{\text{no eggs of any age group at the } i^{th} \text{ station}\}$$

$$= (1 - r_c(i)) \prod_{j=1}^{4} Pr\{Y_{ij} = 0\}$$

$$(22) \quad + r_c(i) \min_j Pr\{Y_{ij} = 0\}$$

This model is used in the next section for the analysis of the 1985 sardine egg survey.

Application to the 1985 Sardine Egg Survey

The methodology developed in the previous section was applied to the data for the 1985 sardine egg survey, conducted in May 1985 by P. Wolf (California Department of Fish and Game) and one of us (P. E. Smith). In that survey, 419 CalCOFI stations were sampled and 11 of those stations (Fig. 1) had sardine eggs of any age group. The total number of eggs discovered was 86. The stated objective of the survey was to determine whether the spawning biomass exceeded 20 000 short tons. The data thus consist of $N_n = 408$ and $N_p = 11$. From those data, the objective was to estimate the maximum likelihood value of m and the probability that m exceeded the critical value m_c.

The multiple age group model was used for calculations, with the $\{m_j, k_j\}$ given above. Other parameters were set at $\alpha p = 1/20$, $b = 0.6$, and $m_c = 1.14$. These are justified as follows. Based on historical records (from the period of the cannery heyday), a sardine spawning biomass of 20 000 short tons covered about 5% of the long-term spawning area (Kramer and Smith 1971; Lasker 1985, p. 18). We thus set $p = 0.05$ and $\alpha = 1$ (note, of course, that only the product αp enters into the computations); the choice $\alpha = 1$ means that if eggs are abundant enough they will be detected. We choose $b = 0.6$ as an upper bound on the effectiveness of the sampler. The value of m_c was also determined by comparison with historical data from the cannery period. We performed computations for $r_c(i)$ constant for all i and in the range of 0.4–1.0. The MLEs obtained in this manner ranged between 1.2 (for $r_c(i) = 0.4$) and 12.5 (for $r_c(i) = 1.0$); the probability that m exceeded the critical level m_c was high for all combinations of parameters tested.

Wolf and Smith (1986) used a method based on egg production and concluded, using the same data, that the spawning biomass exceeded 20 000 short tons and recommended opening a small, directed fishery on sardine in 1986. The "inverse egg production method" used by Wolf and Smith is motivated as follows. The egg production method (Parker 1980; Picquelle and Hewitt 1983; Hewitt 1984; Lasker 1985) is used to estimate spawning biomass B by

$$(23) \quad B = P_0 A\, kW/RFS$$

where P_0 is daily egg production (eggs/0.05 m^2/d), W is average female weight, R is sex ratio of the population, F is batch fecundity (number of eggs spawned/female/batch), S is the proportion of females spawning per day, A is the total area of the survey, and k is a conversion factor from grams to short tons.

Wolf and Smith (1985) invert Eq. (22) (hence the name inverse egg production method IEPM) and argue as follows: if the spawning biomass exceeds B_c short tons, then the area with eggs should exceed a critical area A_c given by

$$(24) \quad A_c = B_c\, RFS/P_0 kW$$

To employ the IEPM, one multiplies the number of stations with positive egg samples by the area associated with each station (in this case, the area is 40 nm^2) and compares that area with A_c. In particular, using the inverse egg production method, Wolf and Smith estimated that a population of 20 000 short tons spawning biomass would cover about 500 nm^2; they estimated that in 1985 the population covered about 670 nm^2. Thus, for the first time since 1974 a directed fishery for sardine opened on 1 January 1986 (Wolf and Smith 1986). It should be noted that many of the parameters in Eq. (23) have considerable uncertainty (Wolf and Smith 1986; Mangel 1988) and this affects the confidence that one has in the estimate.

The IEPM and the methods developed in this paper are similar in spirit, since the objective of each method is to use presence/absence data to determine the spawning biomass of the stock. Although the two methods use the same kind of data, they are different in methodology (the IEPM is fundamentally deterministic while the methods of this paper are fundamentally stochastic). Both methods are easily employed using a small, desktop microcomputer. In a sense then, one has the best possible situation: the IEPM and the methods developed in this paper are two relatively independent analytical procedures for assessing the size of the spawning biomass from the same data. They thus complement each other and can be used to check one another.

Finally, both methods are ideally suited to the situation in which the spawning biomass is sufficiently small that using actual counts is not advisable. For example, analogous egg surveys are currently performed for anchovy, but use counts instead of presence–absence.

When are Counts Preferable to Presence–Absence Sampling?

The alternative to presence–absence sampling is the use of counts, that is records of the actual values of X_i, rather than whether or not $X_i > 0$. In this section, we develop a method that can be used to determine when using counts is preferable to using presence–absence sampling, in the sense that one has a smaller error than the other.

We consider the situation in which all stations have the same values for the detection parameters and the probability of the station being a habitat. In that case, with Y_i denoting the number of eggs in the sample

$$(25) \quad Pr\{Y_i = 0\} = 1 - \alpha p + \alpha p\, \{k/(k+mw)\}^k$$

The MLE for presence–absence sample, henceforth denoted by m_{mle} is given by Eq. (15). Another commonly used estimate of m from presence–absence sampling (Southwood 1976) uses the fraction of zeros $f_o = N_n/N$ in the sample. This is essentially a moment estimator. Assuming that k is constant, equating f_0 to

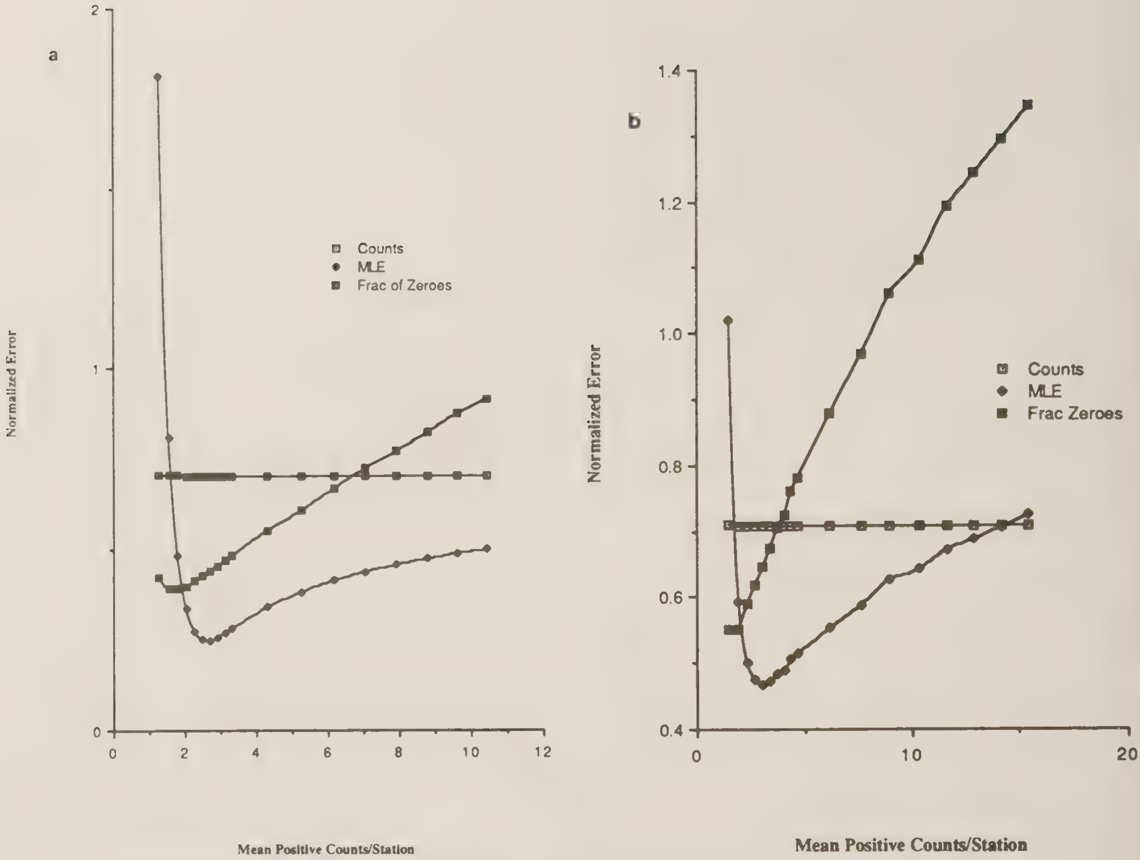

FIG. 4. The normalized errors for the three estimation methods as a function of the number of eggs per positive station. (a) $N = 400$, $\alpha p = 0.3$, and $k = 0.1$, (b) $N = 400$, $\alpha p = 0.3$, and $k = 0.2$.

the right hand side of Eq. (25) and solving for m gives the estimate

$$(26) \quad m_{\text{frac}} = (k/w)\{\alpha p/(f_o - 1 + \alpha p)\}^{1/k} - k$$

Finally, one can estimate m by the mean number of eggs in the samples. Denote this estimate by m_c for count; it is

$$(27) \quad m_c = (1/N)\, \Sigma\, Y_i$$

We consider the situation in which $w = 1$, but $\alpha p < 1$. In light of Eq. (25) we write that

$$(28) \quad Y_i = \begin{cases} 0 \text{ with probability } 1 - \alpha p + \alpha p(k/k+m)^k \\ x \text{ with probability } \alpha p NB(x;m,k) \end{cases}$$

Here $NB(x;m,k)$ denotes the negative binomial probability of x events when the parameters are m and k, so that with probability $1-\alpha p+\alpha p(k/k+m)^k$ no eggs are detected in the sample but when eggs are detected they follow the negative binomial distribution. Using Eq. (27), we see that $E\{m_c\} = \alpha pm$.

To compare these three estimators, we propose using the following normalized error

$$(29) \quad S_i = \{E(m_i - m)^2\}^{1/2}/m$$

in which m_i denotes any of the three estimators and $E\{\ \}$ denotes the expectation over all possible samples. If the m_i were unbiased estimators, then the S_i would be associated coefficients of variation.

When counts are used, S_c can be computed directly and is

$$(30) \quad E\{m_c - m^2\} = (1/N^2)\{N\alpha p(\mathrm{m}^2 + m + \mathrm{m}^2/k) + N(N-1)\alpha^2p^2\mathrm{m}^2\} + m^2 - 2\alpha p\mathrm{m}^2$$

We were unable to develop an analytical formula for m_{mle} or m_{frac}. They are, however, easily computed numerically according to the following scheme. First note that the number of positive samples follows a binomial distribution with number of trials N and success probability $p' = \alpha p - \alpha p(k/k+m)^k$. Let $\mathcal{B}(n;N,p')$ denote the probability of n positive samples for the binomial distribution with parameters N and p'. Then

$$(31) \quad E\{(m_i - m)^2\} = \sum_{n=0}^{N} (m_i(n) - m)^2\, \mathcal{B}(n;N,p')$$

In this equation, $m_i(n)$ is the appropriate estimator when the number of positive samples is n. The right hand side of Eq. (31) is most easily evaluated by noting that Prob $\{N_p=0\} = (1-p')^N$ and that for $n>0$.

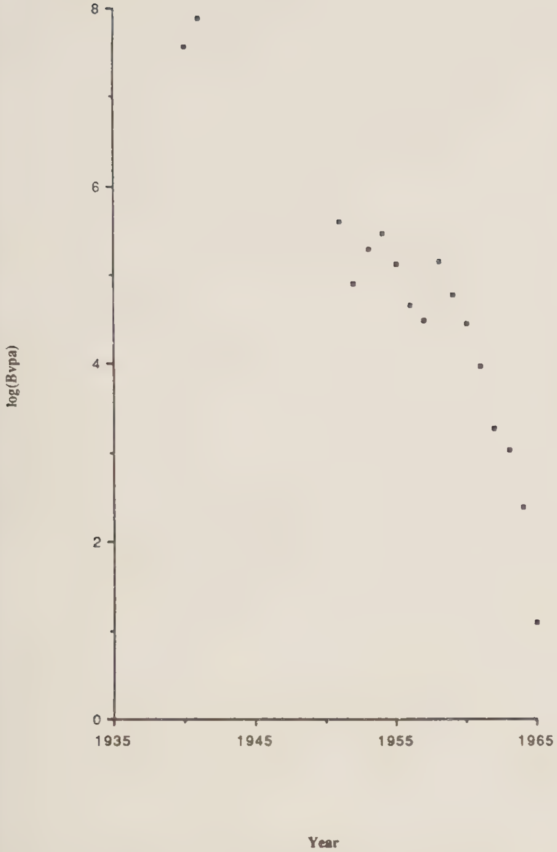

FIG. 5. Estimated spawning biomass B_{vpa} (short tons) of Pacific sardine, 1940–41 and 1951–65. The spawning biomass was estimated by Virtual Population analysis (Smith 1990).

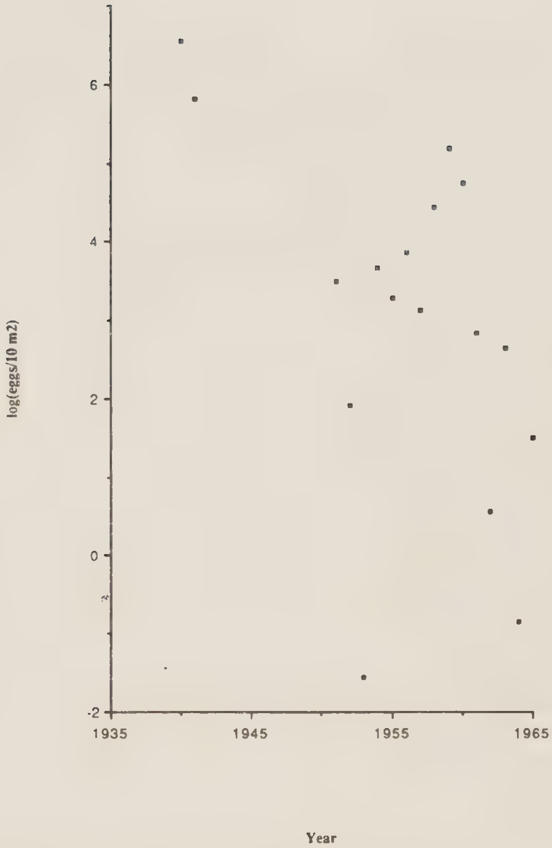

FIG. 6. Egg density (number of eggs/ 10 m^2 sea surface) for the same period as in Fig. 7. Note that there are years in which spawning biomass is very low but in which egg density nearly equals the egg density when the biomass was high.

$$(32)\quad \text{Prob}\,\{N_p = n+1\} = [(N-n)/(x+1)][p'/(1-p')]\;\text{Prob}\,\{N_p = n\}$$

One complication, however, remains. In real surveys, one does not know the value of m. What will be known is the mean number of eggs per positive station. From the definition of conditional probability and Eq. (29)

$$(33)\quad Pr\{Y_i = x \mid Y_i > 0\} = Pr\{Y_i = x,\, Y_i > 0\}/Pr\{Y_i > 0\} = NB(x;m,k)/(1 - (k/k+m)^k)$$

Thus, the mean number of counts per positive station is estimated by

$$(34)\quad E\{Y_i \mid Y_i > 0\} = \Sigma_{x=1}\, x\, NB(x;mk,)/(1-(k/k+m)^k) = m/(1-(k/k+m)^k)$$

Note that this mean is independent of αp; this happens because one is only considering stations with positive counts.

Figure 4 shows the normalized errors as a function of the expected mean number of counts per positive station and suggests that when m is very small, presence–absence sampling using the estimate based on the fraction of zeroes is most preferable, that for intermediate values of m presence–absence sampling using the MLE is best, and that for larger m, counts may be preferable (e.g. Fig. 4b). We stress that these results depend upon parameter values, and that one should repeat the computations for his or her own particular parameter values. The computational schemes outlined in Eq. (25)–(33) are, however, easily implemented on desk-top microcomputers.

A Case Study of Sardine

To justify a number of the assumptions used in this paper, we summarize the results of a study by one of us (Smith 1990) on a long time series for sardine in the California current.

The time series tracked sardine population size as it declined from about 2×10^6 t in 1940 (Murphy 1966) to about 3×10^3 t in the mid-1960s (MacCall 1979). For the period of interest, we show the biomass B_{vpa} estimated by virtual population analysis (Fig. 5), the estimated number of eggs per unit area (Fig. 6), and the percent positive stations (Fig. 7). Note the relatively large estimates for the number of eggs per unit area and the considerable fluctuations in percent positive stations during a period in which the biomass consistently declined. For example, in 1941, when the biomass B_{vpa} = 2709 t, the egg estimate is 337 eggs/10 m^2 while in 1959, when B_{vpa} = 122 t,

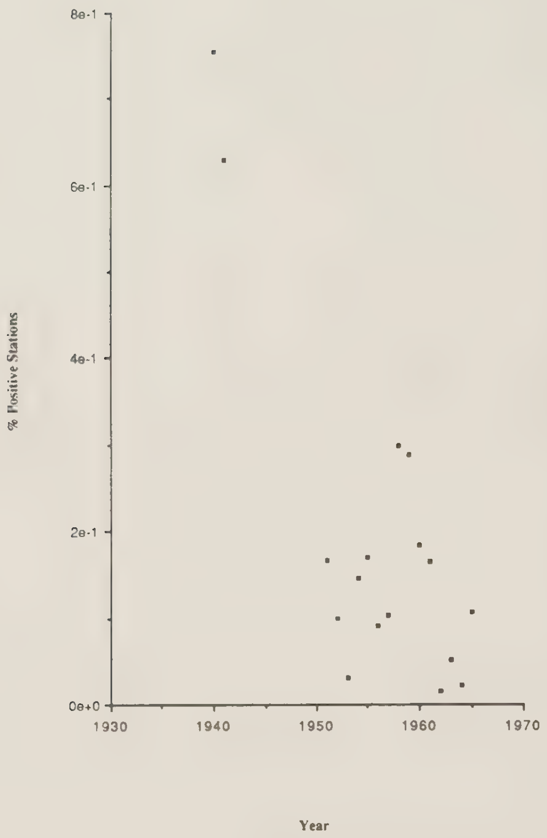

FIG. 7. Percent positive stations for the same period as in Fig. 6. The difficulties identified in Fig. 6 do not occur for this measure of presence–absence sampling.

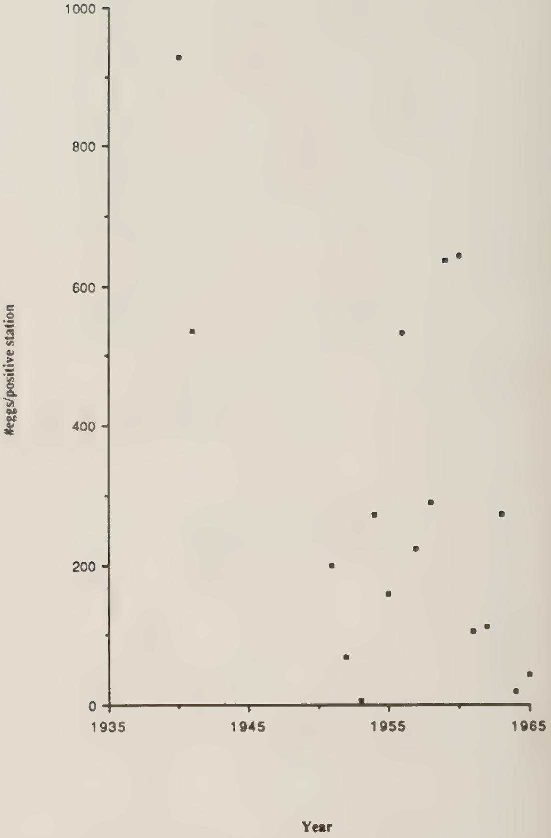

FIG. 8. Number of eggs per positive station for the same period as in Fig. 7. Note that the difficulties identified in Fig. 6 reoccur here, when actual counts are used.

the egg estimate is 182 eggs/10 m^2. That is, the biomass dropped by a factor of about 20 and the average estimate of eggs per unit area dropped by 2. We believe that this is caused by the clumped distribution of the eggs. The generally high values of eggs per positive station (Fig. 8) between 1955 and 1960 are an example of how counts of eggs per positive station can bias the estimation. For example, in 1941 (B_{vpa} = 2709 t) the number of eggs per positive station was 536 and in 1956 (B_{vpa} = 108 t) the number of eggs per positive station was 532. These results suggest that counting eggs may give incredibly misleading estimates of biomass under circumstances that could be reasonably expected to occur and that practicable alternatives such as presence–absence sampling are important.

Smith (1990) used a combination of Virtual Population Analysis (VPA) and regression. The results of this work that are relevant to ours include the following. The apparent relationship between spawning biomass, B_{vpa}, and eggs per unit area is

$$(35)\quad B_{vpa} = 44.3 + 3.43\,E$$

where B_{vpa} is the sardine biomass over 2 yr old and E is the estimate of eggs per unit surface area (number/10 m^2). The r^2 corrected for sample size is 63.8% and the constant is not significant, suggesting that our assumption of a linear relationship between spawning biomass and mean egg density is justified. When the analysis is done without the constant, the relationship becomes B_{vpa} = 3.5419 E. By inverting Eq. (34), it is possible to determine the critical level of egg density associated with a critical level of biomass, as required by the analysis in previous portions of the text.

For an analysis in which the number of square miles covered (E_a) and the number of eggs per positive station (E_{pos}) are separated, the results of the regression are

$$(36)\quad B_{vpa} = -187.8 - 0.6918\,E_{pos} + 112.43\,E_a$$

Neither the constant nor the coefficient of E_{pos} are significant. The r^2 for the model (36) is 79.1%. Excluding both the constant and the coefficient of E_{pos} gave the relationship B_{vpa} = 74.367 E_a, justifying the assumptions of the inverse egg production method and the interpretation of our results that presence–absence sampling provides a good measure of areal coverage.

Similar results are obtained when larval data are used, with higher values of r^2. We believe that this is caused by a longer period in which the larvae are vulnerable to a survey (20 d for larvae vs. 3 d for eggs). In addition, there is excellent corre-

TABLE 4. Mean number of sardine eggs per positive tow for Pacific sardine 1931–89.

Sampling device	Mean number of eggs per positive station	Sardine biomass (million m-tons)
California Dept. of Fish and Game 2 m silk ring net (1931–32)	543	3.50[a]
One metre silk ring net (1941)	568	2.50[b]
Half-meter silk ring net (1941)	618	2.50[b]
High-speed net (1950)	405	0.70[b]
CalCOFI standard net (1-m ring net) 1951–79)	476	<0.30[b]
Bongo net (1977–89)	397	<0.02
CalCOFI vertical egg net (CalVET) 1985–86	932	0.02
Simulation using a log-normal distribution with mean 3.7 and SD 2.14, based on eggs/positive tow 1951–89	416	Not applicable

[a] Murphy (1966).
[b] MacCall (1979).

lation between overall larval abundance and overall egg abundance.

Finally, we compiled essentially all of the sampling information for Pacific sardine over the last half-century (Table 4). The results of a simulation study of sampling, using the data on number of eggs per positive station from 1951–89, show that the mean number of sardine eggs per positive tow is very insensitive to the spawning biomass of the sardine and the type of net used to sample the sardine eggs (Table 4). Thus the results suggest that the area of spawning (or fraction of spawning ground covered) is most sensitive to spawning biomass in this species. All of the sample means in Table 4 could have been derived from random samples from a population in which the number of eggs per positive station was log-normally distributed with mean 3.7 and standard deviation 2.14, as in the last line of Table 4. A study of the sampling distributions, not presented in Table 4, showed that the upper limit of the number of sardine eggs per positive station was nearly uniform for all samplers and biomass levels. The lower limit is controlled by the threshold of the sampler. For example, one sardine egg in a CalVET sampler (area 0.05 m^2) corresponds to 200 eggs per 10 m^2, whereas 1 sardine egg in a Bongo net is five sardine eggs per 10 m^2, and one sardine egg in the CalCOFI standard net is three sardine eggs per 10 m^2.

Conclusions

Our objective was to introduce a new method for the analysis of egg or larval sampling for purposes of biomass estimation. Presence–absence sampling has a number of points that will help facilitate fisheries management. First, when compared to full fishing surveys for stock estimation, presence–absence sampling is a relatively inexpensive means of gaining information about the managed stock. For example, one can use presence–absence sampling and the methods in this paper to determine if the probability that the stock is sufficiently strong to warrant a full biomass survey. Second, presence–absence sampling provides a natural determination of the management boundaries of the stock. Third, the method has wide applicability. Fourth, the method requires a minimum amount of data and parameters and nicely complements other methods for estimating spawning biomass.

When a stock is recovering, as in the case of sardine, a variety of estimation techniques are needed for the successful management of the recovery. Early on, a relatively simple and inexpensive but cautious technique such as presence–absence sampling is valuable. During this period one wants to build confidence both in the estimation methodology and in the recovery of the stock. Afterwards, more expensive assessment techniques such as the egg production method become useful as a means of accurately quantifying the stock level. When the stock is sufficiently recovered and strong, one can use techniques that interpolate between years in which expensive assessment methods are used.

There are a number of directions for future work. The most important or promising are the following ones.

Joint estimation of habitat boundaries and the biomass — In general, the boundary of the geographical habitat will not be known and one simultaneously estimates the distribution of the mean of the biomass and the probability that a site is a habitat. Wolf and Smith (1985, table 2, p. 137) give an illustration of the importance of habitat exit information. As spawning population increases, the spatial spread of the stock may increase (Rosenzweig 1981; MacCall 1988). MacCall (1984, 1988) shows how to compute the spawning habitat suitability contours for the northern anchovy *Engraulis mordax*. These contours represent average phenomena and in any given year one will not know the location of the habitat contours precisely. Operationally, then, the long term average habitat contours can be used to plan the initial part of the sea survey, but then the presence–absence data are used to update (e.g. in a Bayesian sense (Mangel 1985b, 1988)) the estimation of the contours. The natural extension of these ideas is adaptive survey optimization (Walters 1986): one develops an ''adaptive survey design'' in which the data that have been accumulated thus far in the survey are used to determine where future sampling occurs. The sampling process $\{Y_{ij}\}$ is now viewed as a spatial point process and one is attempting to control properties of this spatial point process.

Egg surveys as priors and economic modeling — If one decides that the spawning biomass does exceed the critical level, then a full biomass (i.e. sampling of juvenile and adult fish) survey may be warranted. In such a case, the egg survey can be used as a prior spatial distribution when planning the full biomass survey. In addition, the results of the presence–absence egg survey can be used to determine the economic costs and benefits of a complete biomass survey and of not allowing commercial fishing if the spawning biomass exceeds an appropriate level. Thus, the presence–absence survey fits nicely into the overall bioeconomics of fisheries management.

We believe that presence-absence sampling provides a new tool for the estimation of the biomass of pelagic fish stocks.

The great advantages of presence–absence sampling is that it can be used in situations in which other methods are either too expensive or unreliable and thus provides a technique that complements existing ones.

Acknowledgments

This work represents the results of an ongoing collaboration with Patricia Wolf, California Department of Fish and Game. For comments and discussion on the analytical methods, we thank L. Botsford, D. Ludwig, M. Rosenzweig, and C. Walters. Previous versions of the manuscript were critically read by L. Botsford, J. Carscadden, C. Clark, I. Hampton, S. Picquelle, P. Shelton, and G. Stauffer; their comments are greatly appreciated. This work was partially supported by NSF Grant MCS81-21659, by the University of California Agricultural Experiment Station, and by NOAA, National Sea Grant Program, Department of Commerce, under Grant Number NA85AA-D-56140, Project Number R/F-109, through the California Sea Grant Program. The U.S. government is authorized to reproduce it and distribute it for governmental purposes.

References

ANSCOMBE, F. J. 1984. The transformation of Poisson, binomial and negative binomial data. Biometrika 35: 256–254.

1950. Sampling theory of the negative binomial and logarithmic series distributions. Biometrika 37: 358–382.

BISSELL, A. F. 1972. A negative binomial model with varying element sizes. Biometrika 59: 435–441.

BLISS, C. I., AND A. R. G. OWEN. 1958. Negative binomial distributions with a common *k*. Biometrika 45: 59–68.

DEBOUZIE, D., AND J. THIOULOUSE. 1986. Statistics to find spatial and temporal structures in populations, p. 263–282. In M. Mangel, J. R. Carey, and R. Plant [ed.] Pest Control: Operations and Systems Analysis in Fruit Fly Management. Springer–Verlag, Heidelberg.

DENNIS, B., AND G. P. PATIL. 1984. The gamma distribution and weighted multimodal gamma distributions as models of population abundance. Math. Biosci. 68: 187–212.

DIGGLE, P. J. 1983. Statistical Analysis of Spatial Point Patterns. Academic Press, New York, NY. 148 p.

DOWNING, J. A. 1979. Aggregation, transformation, and the design of benthos sampling programs. J. Fish. Res. Board Can. 36: 1454–1463.

EDWARDS, A. W. F. 1972. Likelihood. Cambridge University Press, Cambridge, UK.

GROSBERG, R. K., AND J. F. QUINN. 1986. The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. Nature (Lond.) 322: 456–459.

HEWITT, R. 1981. The value of pattern in the distribution of young fish. Rapp. P-v. Cons. Int. Explor. Mer 178: 229–236.

1984 spawning biomass of northern anchovy. Administrative Report LJ-84-18. Southwest Fisheries Center, La Jolla, CA.

HEWITT, R., A. BINDMAN, AND N. LO. 1984. Procedures for calculating the egg production estimate of spawning biomass. Admin. Rep. LJ-84-19. Southwest Fisheries Center, La Jolla, CA.

HUDSON, D. J. 1971. Interval estimation from the likelihood function. J. R. Stat. Soc. 33: 256–262.

JOHNSON, N., AND S. KOTZ. 1969. Discrete Distributions. Wiley Interscience, New York, NY. 328 p.

KRAMER, D., AND P. E. SMITH. 1971. Seasonal and geographic characteristics of fishery resources. California current region — VII. Pacific Sardine. Comm. Fish. Rev. 33: 7–11.

LASKER, R. 1981. Marine Fish Larvae. Washington Sea Grant Publications, University of Washington Press, Seattle, WA. 131 p.

1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS 36, US Department of Commerce, Springfield, VA.

MACCALL, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Cal. Coop. Oceanic Fish. Invest. Rep. 20: 72–82.

1984. Population models of habitat selection, with application to the northern anchovy. Administrative Report LJ-84-01. Southwest Fisheries Center, La Jolla, CA.

1988. Dynamic Geography of Marine Fish Populations. University of Washington Press, Seattle, WA.

MANGEL, M. 1985a. Search models in fisheries and agriculture. Springer lecture notes in biomathematics. Springer-Verlag, New York, NY. 61: 105–138.

1985b. Decision and Control in Uncertain Resource Systems. Academic Press, New York, NY. 255 p.

1987. Sampling highly aggregated populations with application to California sardine management. Springer lecture notes in biomathematics. Springer-Verlag 72: 247–263.

1988. From egg surveys to ecosystem models: biological assumptions in fisheries management. Springer lecture notes in coastal and estuarine studies. Springer-Verlag 28: 75–102.

MURPHY, G. I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34(1): 1–84.

PARKER, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull. 78: 541–544.

PENNINGTON, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. Biometrics 39: 281–286.

PERRY, J. N., AND L. R. TAYLOR. 1986. Stability of real interacting populations in space and time: implications, alternatives, and the negative binomial k_c. J. Anim. Ecol. 55: 1053–1068.

PICQUELLE, S. J., AND R. P. HEWITT. 1983. The northern anchovy spawning biomass for the 1982–83 California fishing season. Cal. Coop. Oceanic Fish. Invest. Rep. 24: 16–28.

PIELOU, E. C. 1977. Mathematical Ecology. John Wiley and Sons, New York, NY. 385 p.

RESH, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. J. Fish. Res. Board Can. 36: 290–311.

RIPLEY, B. D. 1981. Spatial Statistics. Wiley Interscience, New York, NY. 252 p.

ROSENZWEIG, M. 1981. A theory of habitat selection. Ecology 62: 327–335.

SAMPFORD, M. R. 1956. The truncated negative binomial distribution. Biometrika 42: 58–69.

SANTANDER, H., P. E. SMITH, AND J. ALHEIT. 1982. Determination of sampling effort required for estimating egg production of anchovata, *Engraulis ringens*, off Peru. Inst. Mar Peru Bol. 7: 5–18.

SEBER, G. A. F. 1973. The Estimation of Animal Abundance and Related Parameters. Griffin, London, UK. 506 p.

SETTE, O. E., AND E. H. AHLSTROM. 1948. Estimation of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. Sears Found. J. Mar. Res. 7: 511–542.

SMITH, P. E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 164: 282–292.

1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P-v. Cons. Int. Explor. Mer. 173: 117–127.

1990. Monitoring of Pacific sardine (*Sardinops sagax*) interannual changes of spawning biomass. Cal. Coop. Oceanic Fish. Invest. Rep. (In press)

SMITH, P. E., AND R. P. HEWITT. 1985. Anchovy egg dispersal and mortality as inferred from close-interval observations. Cal. Coop. Oceanic Fish. Invest. Rep. 26: 97–110.

SMITH, P. E., AND S. L. RICHARDSON. 1977. Standard techniques for pelagic fish egg and larva studies. FAO Fish. Tech. Pap. 175, Food and Agriculture Organization of the United Nations, Rome, Italy.

SOUTHWOOD, T. R. E. 1976. Ecological Methods. Chapman and Hall, London, UK. 524 p.

SQUIRE, J. L. 1983. Abundance of pelagic resources off California, 1968–73, as measured by an airborne fish monitoring program. NOAA Tech. Rep. NMFS SSRF-762, Rockville, MD.

TAYLOR, C. C. 1953. Nature and variability in trawl catches. Fish. Bull. U.S. Fish and Wildlife Service Washington, DC. 54: 145–166.

TAYLOR, L. R., WOIWOD, I. P., AND J. N. PERRY. 1979. The negative binomial as a dynamic ecological model for aggregation and the density dependence of *k*. J. Anim. Ecol. 48: 289–304.

VLYMEN, W. J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior. Env. Biol. Fish. 2: 211–233.

WALTERS, C. 1986. Adaptive Management of Renewable Resources. MacMillan Publishing Co, New York, NY.

WOLF, P., AND P. E. SMITH. 1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Cal. Coop. Oceanic Fish. Invest. Rep. 26: 130–138.

1986. The relative magnitude of the 1985 Pacific sardine spawning biomass off southern California. Cal. Coop. Oceanic Fish. Invest. Rep. 27: 25–31.

WOLF, P., P. E. SMITH, AND C. L. SCANNELL. 1987. The relative magnitude of the 1986 Pacific sardine biomass off California. Cal. Coop. Oceanic Fish. Invest. Rep. 28: 21–26.

ZWEIFEL, J. R., AND P. E. SMITH. 1981. Estimates of abundance and mortality of larval anchovies (1951-75): Application of a new method. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178: 248–259.

Appendix A: Alternative Choices for the Underlying Distributional Model

We briefly describe other aggregated distributional models that could be used instead of the Negative Binomial model chosen for the main part of the text. These models all have the property that, depending upon parametrization, the probability of a zero is very high and the variance may greatly exceed the mean.

For the Neyman type A distribution (Johnson and Kotz 1969)

$$\begin{aligned}&Pr(X_i = x| \text{ station is a habitat}\} =\\ \text{(A.1)}\quad &\Sigma_{j=1} [e^{-\lambda}\lambda^j/j!][e^{-j\theta} (j\theta)^x/x!]\end{aligned}$$

with the properties that

$$\begin{aligned}&Pr\,\{X_i = 0| \text{ station is a habitat}\} = \exp(-\lambda\,(1 - e^{-\theta}))\\ \text{(A.2)}\quad &E\{X_i| \text{ station is a habitat}\} = \lambda\theta\\ &\mathrm{Var}\{X_i| \text{ station is a habitat}\} = \lambda\theta(1 + \theta)\end{aligned}$$

For the Polya–Eggenberger distribution (Johnson and Kotz 1969)

$$\begin{aligned}&Pr\{X_i = x| \text{ station is a habitat}\} =\\ \text{(A.3)}\quad &\frac{\binom{n}{x} \prod_{j=0}^{x-1} (P + j\alpha) \prod_{j=0}^{n-x-1} (Q + j\alpha)}{\prod_{j=0}^{n-1} (1 + j\alpha)}\end{aligned}$$

In this equation, P, n, and α are parameters and $Q = 1 - P$. For this distribution

$$\begin{aligned}&E\{X_i| \text{ station is a habitat}\} = nP\\ \text{(A.4)}\quad &\mathrm{Var}\{X_i| \text{ station is a habitat}\} = nPQ(1 + n\alpha)/(1 + \alpha)\end{aligned}$$

In the limit that $n \rightarrow \infty$, $P \rightarrow 0$, $\alpha \rightarrow 0$ such that nP and $n\alpha$ are bounded and nonzero, the Polya distribution is approximated by the *NB*. Johnson and Kotz (1969) also note that the Polya distribution is obtained as the unconditional distribution when a variable is conditionally binomial and the parameter p of the binomial distribution has a beta density.

A third model is the ''zero/random'' model. Suppose that a station has a positive number of eggs with probability p and that if a station has a positive number of eggs, then the egg number is distributed according to the positive terms of a Poisson process. Then

$$\begin{aligned}&Pr\{X_i = 0| \text{ station is a habitat}\} = 1 - p\\ \text{(A.5)}\quad &Pr\{X_i = x > 0| \text{ station is a habitat}\} =\\ &\qquad [p/e^\lambda - 1]\,[\lambda^x/x!]\end{aligned}$$

The second of these equations arises in the following manner: X_i is positive with probability p. If it is, then its distribution is Poisson, excluding the zero term. This leads to the $\lambda^x/x!$. The normalization constant is then $\Sigma_{x=1} \lambda^x/x! = e^\lambda - 1$. The first two moments of this distribution are

$$\begin{aligned}&E\{X_i| \text{ station is a habitat}\} = p\lambda e^\lambda/(e^\lambda - 1)\\ \text{(A.6)}\quad &E\{X_i^2| \text{ station is a habitat}\} = pe^\lambda(\lambda + \lambda^2)/(e^\lambda - 1)\end{aligned}$$

9033

Biology and Potential Use of Pacific Grenadier, *Coryphaenoides acrolepis*, off California

TETSUO MATSUI, SUSUMU KATO and SUSAN E. SMITH

ABSTRACT—Grenadiers (family Macrouridae) are the most abundant fish on most continental slope areas worldwide. Off California the Pacific grenadier, Coryphaenoides acrolepis, *occurs in relatively large numbers and may have marketing potential. This report provides information on the biology of the species and catch results from a number of scientific cruises. Catch data on several other species found together with Pacific grenadier, particularly sablefish,* Anoplopoma fimbria, *are also given. The fish were caught with a bottom trawl (15 trawls), and with free-vehicle longline gear (117 sets). The latter was a hook and line system in which the gear was dropped to the sea floor untethered to the fishing vessel, and floated to the surface, with the catch, when detachable weights were automatically released. Sablefish dominated longline catches in depths of 200-600 fm (334-1,098 m), while Pacific grenadier was most abundant between 600 and 1,000 fm (1,098-1,830 m). Best trawl catches of Pacific grenadier were made at depths between 615 and 675 fm (1,125 and 1,235 m) and at 760 fm (1,391 m).*

Ripe females were absent from our samples, but spent females were found during the entire year with highest numbers in the spring and early summer. Only one larva was found despite extensive sampling with plankton nets.

Pacific grenadier was found to have good edible qualities by a taste-test panel, although the protein content (15 percent) and flesh yield (24 percent) were significantly lower than those of other fishes. A second species, the giant grenadier, Albatrossia pectoralis, *was found to have exceptionally poor eating qualities and even lower protein content.*

Introduction

Grenadiers (also known as rattails) belong to the family Macrouridae, and are related to the codfishes (family Gadidae). They are among the most abundant fishes in continental slope and abyssal waters worldwide. The majority of macrourid species appear to spend a good part of the time swimming near the ocean bottom, feeding on benthic and midwater organisms (Marshall and Merrett, 1977). About 300 species are known, of which 11 inhabit the deep waters off California[1].

Although abundant, grenadiers are not utilized to a great extent. The remoteness of their habitat and the small size, soft flesh, and low meat yield of many species have discouraged their commercial use. A few species with good flesh characteristics are presently sold as food fish, while others are used as fish meal and fertilizer. In the northeast and northwest Atlantic over 65,000 metric tons (t) of one species, the roundnose grenadier, *Coryphaenoides rupestris*, were caught in 1975 (FAO, 1979). Although the catch of this species has declined substantially, other species are starting to be utilized, and the total grenadier catch in 1986 was around 60,000 t, 54 percent of which was roundnose grenadier (FAO, 1988). Commercial landings in the northeast Pacific have been minimal, even though macrourids are the most abundant fishes found in trawl catches in deep waters off Oregon and Washington (Alton, 1972; Pearcy and Ambler, 1974).

Off California, at least three species of grenadier appear to be of sufficient size and abundance to warrant marketing consideration. These are the Pacific grenadier, *Coryphaenoides acrolepis*; abyssal grenadier, *C. armatus*; and giant grenadier, *Albatrossia pectoralis*. The Pacific grenadier (Fig. 1) appears to have the best potential, as the quality of its flesh is good and it is abundant off California. The largest specimen of *C. acrolepis* we have measured was over 95 cm (37 inches) in total length. It weighed 4 kg (8.8 pounds) and was taken at lat. 29°31.3′N, long. 117°12.0′W at a depth of 1,050 fm (1,920 m). This may have been an unusually large individual, as the prior known record length for the species is smaller at 87 cm or 34 inches (Rass, 1963, in Iwamoto and Stein, 1974). Pacific grenadier is a smaller species than the other two grenadiers. Its skin is dark and covered with adherent, rough scales. The long tapering tail, characteristic of all grenadiers, contributes to a low percentage yield of flesh compared with other fishes.

The giant grenadier (Fig. 2) is the largest of all of the grenadiers, reaching a length of around 150 cm (5 feet) (Iwamoto and Stein, 1974). Despite the large size and relatively high availability, its commercial potential is limited because

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[1] Tomio Iwamoto, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118. Personal commun.

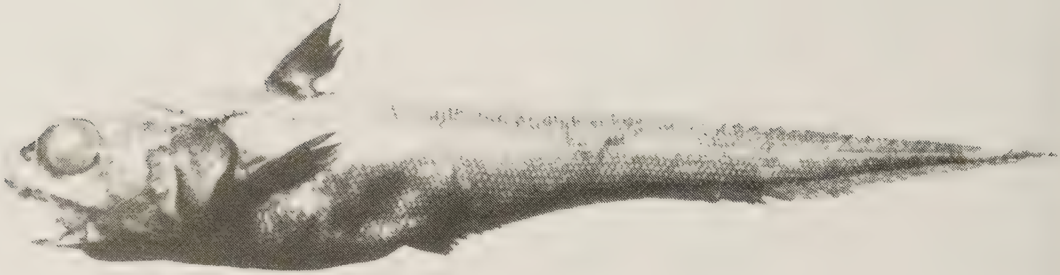

Figure 1.—Pacific grenadier, *Coryphaenoides acrolepis*.

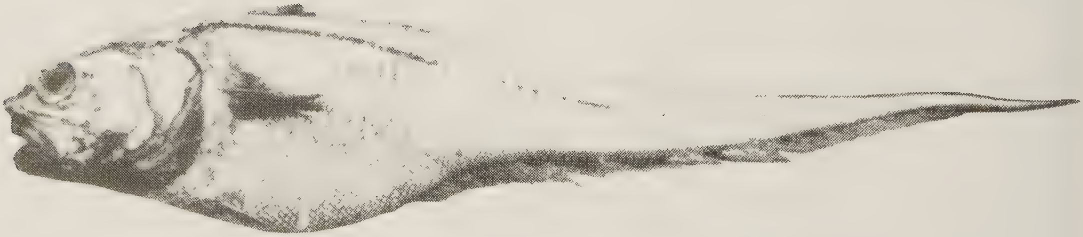

Figure 2.—Giant grenadier, *Albatrossia pectoralis*.

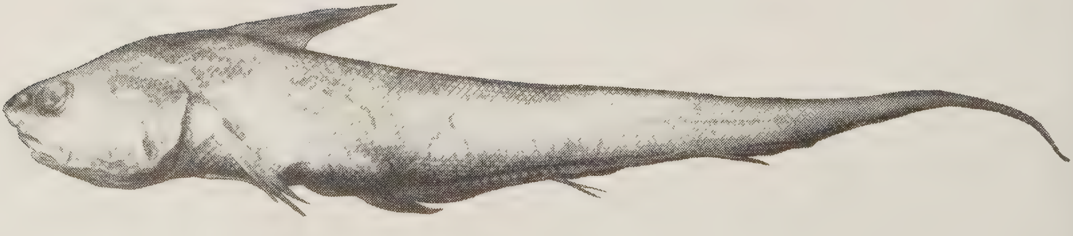

Figure 3.—Abyssal grenadier, *Coryphaenoides armatus*.

Table 1.—Station data (listed by depth) for free-vehicle longline fishing conducted by SIO from 1965 to 1979.

Cruise and station	Date	Lat. (N)	Long. (W)	Depth (fm)	Time started	Hours fished
MV71-I-49	5/30/71	32°22.5′	118°28.1′	153	2316	11.23
MF71-2	7/22/71	32°38.2′	117°57.3′	240	0919	3.37
MV71-I-46	5/30/71	32°06.6′	118°15.6′	293	2046	10.98
MV71-I-50	5/30/71	32°22.2′	118°26.4′	304	2334	10.65
MV71-I-57	5/31/71	32°34.7′	118°00.4′	310	2042	9.68
MV71-I-40	5/28/71	30°16.5′	116°09.7′	320	2132	9.63
MV71-2	7/22/71	32°38.2′	117°57.3′	330	0928	3.28
MV65-III-18	9/24/65	32°44.0′	118°20.8′	337	2130	10.28
MV71-I-52	5/13/71	32°22.4′	118°21.3′	346	0012	11.63
M6-3	8/12/71	32°50.0′	117°31.4′	400	2254	8.68
MV67-II-26	6/16/67	38°00.0′	123°31.0′	400	1915	18.92
SC2-74	11/23/74	32°36.8′	117°28.5′	420	1044	4.40
MV65-II-33	9/26/65	32°40.0′	118°37.5′	426	2144	10.02
M1-2	2/02/71	32°50.0′	117°31.2′	445	2204	9.93
M5-3	7/16/71	32°50.0′	117°31.0′	445	0950	3.75
M3-3	5/13/71	32°50.0′	117°31.0′	445	0735	4.58
MV71-I-24	5/25/71	28°21.8′	115°44.3′	453	2114	11.27
MV67-IA-22	4/26/67	28°09.0′	118°16.2′	455	0218	15.70
MV71-I-16	5/23/71	29°27.5′	117°19.2′	490	2204	12.65
M10-5	2/09/72	32°34.7′	117°26.0′	530	2140	10.33
MV67-IA-28	4/27/67	29°26.5′	117°15.6′	536	1953	11.88
MV65-III-24	9/25/65	32°44.5′	118°43.5′	537	1830	13.00
S2-2	5/08/75	32°50.4′	117°47.9′	550	1635	4.18
M10-6	2/09/72	32°34.5′	117°25.4′	550	2156	9.15
MV65-III-34	9/26/65	32°41.3′	118°39.0′	555	2221	9.90
M9-3	12/21/71	32°26.0′	117°33.7′	555	1935	13.58
MV71-I-58	5/31/71	32°32.8′	117°59.5′	560	2104	10.25
MV67-II-15	6/12/67	36°43.3′	122°03.7′	560	1925	20.38
M8-2	11/01/71	32°26.8′	117°34.0′	561	2212	9.05
MV71-I-51	5/30/71	32°22.2′	118°23.7′	563	2351	11.35
M12-2	9/28/72	32°26.5′	117°33.8′	568	0047	7.52
M9-4	12/21/71	32°26.5′	117°33.5′	595	1945	14.00
M15-5	3/31/74	35°25.0′	121°42.2′	600	0554	3.27
M8-3	11/01/71	32°26.2′	117°33.1′	605	2231	8.90
MV65-III-35	9/26/65	32°41.6′	118°41.0′	610	2253	11.02
M12-3	9/28/72	32°26.7′	117°33.6′	610	0109	6.82
SC74	11/17/74	32°25.8′	117°22.1′	610	1105	4.22
M11-2	4/07/72	32°34.1′	117°26.9′	620	1908	9.12
SC79	11/03/79	32°36.0′	117°28.1′	620	1055	2.00
SC3-74	11/23/74	32°38.2′	117°30.0′	630	1101	7.23
M8-4	11/01/71	32°25.6′	117°32.5′	630	2255	9.92
MV65-III-36	9/26/65	32°42.2′	118°43.8′	631	2324	10.02
M11-4	4/09/72	32°26.4′	117°33.6′	647	0046	6.82
70RI-7	10/29/70	32°34.8′	117°30.0′	655	1810	9.88
MV71-I-17	5/23/71	29°28.9′	117°17.1′	655	2225	13.70
70RI-8	10/29/70	32°35.0′	117°30.0′	656	1820	10.00
SC17	7/22/75	32°34.4′	117°28.5′	660	1045	3.12
MV71-I-4	5/28/71	30°15.5′	116°10.7′	663	2149	10.46
M15-3	3/27/74	32°32.7′	117°34.3′	668	0705	4.77
M15-1	3/26/74	32°28.8′	117°32.1′	670	1203	4.57
M8-6	11/02/71	32°35.0′	118°03.1′	670	2312	9.30
70RI-2	10/26/70	32°25.2′	117°28.9′	680	2230	10.92
70RI-3	10/26/70	32°25.2′	117°28.9′	680	2250	11.50
70RI-4	10/26/70	32°25.2′	117°28.9′	680	2304	15.43
71RI-1	1/18/71	32°27.0′	117°29.1′	680	2110	5.33
M4-1	6/22/71	32°29.6′	117°28.6′	680	1832	13.70
M4-2	6/22/71	32°29.8′	117°28.6′	680	1832	15.70
M5-1	7/05/71	32°25.2′	117°29.0′	680	1058	4.03
M6-1	8/10/71	32°24.8′	117°28.8′	680	1110	8.92
M7-1	9/13/71	32°25.2′	117°28.9′	680	2337	8.97
M9-1	12/20/71	32°24.8′	117°29.0′	680	2258	13.43
M9-2	12/20/71	32°25.1′	117°29.1′	680	2340	12.75
M10-2	2/07/72	32°25.8′	117°28.0′	680	2348	12.27
M10-4	2/09/72	32°26.4′	117°33.5′	680	0005	14.50
M11-3	4/08/72	32°24.8′	117°28.6′	680	2345	7.00
M12-1	9/27/72	32°24.9′	117°29.0′	680	0019	9.17
M13-1	2/28/73	32°25.5′	117°28.9′	680	2325	9.00
MV67-IA-3	4/20/67	31°29.0′	118°01.0′	690	2025	12.58
SC75	—	32°34.9′	117°26.7′	700	1343	3.53
MV71-I-47	5/30/71	32°08.8′	118°17.0′	702	2102	11.13
MV71-I-11	5/20/71	28°52.7′	118°12.2′	710	1937	11.88
S2-1-1	5/06/75	32°28.2′	118°48.5′	710	0725	5.92
MV65-III-37	9/22/65	32°42.6′	118°46.0′	712	0013	10.10
MV71-I-10	5/20/71	28°55.0′	118°11.4′	715	2006	10.63
M2A1	4/13/71	31°51.0′	117°11.7′	730	2153	10.32
M2A2	4/13/71	31°51.0′	117°11.7′	730	2110	11.95
71RI-2	1/19/71	32°45.2′	119°26.5′	735	2110	11.58
MV65-III-19	9/24/65	32°42.0′	118°16.0′	738	2317	9.30
MV65-III-26	9/25/65	32°47.6′	118°47.0′	748	1936	13.07
MV71-I-3	5/18/71	28°52.2′	118°12.0′	750	2106	10.04
MV71-I-59	5/31/71	32°31.8′	117°58.7′	765	2124	10.43
MV67-II-16	6/12/67	36°42.8′	122°03.5′	790	1947	16.43
MV65-III-3	9/21/65	30°52.0′	118°07.6′	790	1746	17.40
MV65-III-38	9/27/65	32°43.0′	118°48.5′	798	0050	9.83
MV67-II-28	—	37°59.0′	123°34.0′	800	2007	19.75
MV65-I-5	6/10/65	28°51.0′	115°46.7′	814	1851	15.05
M8-7	11/02/71	32°35.0′	118°03.1′	850	2340	10.00
MV67-1A-9	4/22/67	30°47.2′	117°12.7′	873	1913	12.35
MV71-I-25	5/25/71	28°23.6′	115°47.5′	875	2149	11.02
MV67-IA-7	4/22/67	30°53.3′	117°13.0′	890	0215	6.00
MV65-III-28	9/25/65	32°50.6′	118°52.0′	896	2055	14.07
MV67-IA-18	4/24/67	29°35.3′	117°18.1′	900	2301	14.40
MV65-III-29	9/25/65	32°51.2′	118°54.8′	916	2207	12.05
M1-3	2/01/71	32°30.1′	118°11.4′	925	2142	11.05
M3-2	5/12/71	32°30.5′	118°11.5′	925	2130	4.13
M5-2	7/15/71	32°30.0′	118°11.5′	925	1956	9.00
M8-5	11/02/71	32°30.0′	118°11.4′	930	2158	9.53
M6-2	8/11/71	32°30.1′	118°11.7′	937	0903	8.18
MV71-I-42	5/28/71	30°11.5′	116°12.5′	938	2229	10.23
MV65-III-21	9/25/65	32°40.3′	118°11.8′	952	0015	9.88
M7-3	9/14/71	32°30.0′	118°11.0′	980	2351	9.02
MV71-I-48	5/30/71	32°12.4′	118°14.1′	998	2138	10.88
MV65-III-4	9/21/65	30°50.4′	118°08.7′	1017	1842	16.55
MV67-IA-20	4/26/67	28°08.2′	118°13.3′	1024	0117	16.30
MV71-I-60	6/01/71	32°30.0′	117°57.9′	1026	2149	10.27
MV71-I-4	5/18/71	28°52.8′	118°10.8′	1026	2147	10.82
MV71-I-12	5/21/71	28°52.9′	118°10.9′	1039	2001	11.90
MV71-I-19	5/23/71	29°31.3′	117°12.0′	1050	2133	14.73
MV67-IA-10	4/22/67	30°47.0′	117°03.2′	1075	2022	13.53
MV71-I-26	5/25/71	28°25.2′	115°49.7′	1095	2214	11.08
MV67-II-18	6/12/67	36°37.1′	122°09.2′	1200	2118	17.12
MV67-IA-11	4/22/67	30°53.6′	117°04.0′	1208	2103	13.53
MV67-II-29	6/16/67	37°58.0′	123°38.0′	1233	2039	19.68
MV67-IA-16	4/24/67	29°36.6′	117°20.4′	1382	2225	13.72
MV65-III-6	9/21/65	30°36.3′	118°13.4′	1391	2121	16.95
MV67-II-30	6/16/67	37°57.4′	123°40.5′	1480	2103	20.78
SIO66-50	5/21/66	40°34.6′	125°51.4′	1624	1907	13.38

its flesh is extremely soft and watery. This species is frequently taken together with the Pacific grenadier in bottom trawl nets and is reported to have a wide depth range of 110-1,185 fm (200-2,170 m) (Novikov, 1970). Skin color of the giant grenadier is much lighter than that of the other two species, and individuals are usually pale when caught because most of their scales are sloughed off during capture.

The abyssal grenadier (Fig. 3) is dark brown to blackish in color with scales that are much smoother than those of the Pacific grenadier, and has 10-12 pelvic finrays (in Pacific samples) (Iwamoto and Stein, 1974), compared with (mostly) 8 for the Pacific grenadier. It is considered one of the largest grenadiers, with a largest record of 87 cm or 34 inches (Iwamoto and Stein, 1974). *C. armatus* ranges to much greater depths than the other two species. Although the known depth range for the species is between 154 and 2,570 fm (282-4,700 m) (Grey, 1956) only three records came from less than 547 fm or 1,000 m (Marshall, 1973). In the eastern North Pacific they are taken in abundance between 2,000 and 4,000 m (Iwamoto and Stein, 1974). Based on morphological differences, Wilson and Waples (1984) suggested recognition of the North Pacific population as a distinct

Table 2.—Longline fishing conducted on R/V *David Starr Jordan*, September and December 1985.

Cruise and sta.	Date (1985)	Lat. (N)	Long. (W)	Start fishing	Fishing time
Cruise DS85-10(193)					
1	9-19	32°56.3′	118°19.2′	0551h	8.0h
2	9-19	33°13.6′	118°59.1′	2318	6.4
3	9-20	33°05.8′	119°17.3′	2328	6.8
4	9-23	35°02.6′	121°41.5′	2343	6.2
5	9-26	32°28.7′	118°48.0′	0832	5.8
Cruise DS85-121(195)					
6	12-5	34°57.8′	121°35.1′	0032	8.0
7	12-6	35°09.4′	121°48.2′	0000	8.0
8	12-6	35°42.9′	122°11.8′	2306	7.2
9	12-9	36°55.2′	122°34.7′	1105	6.8
10	12-10	36°26.9′	122°06.3′	1106	8.0
11	12-11	37°01.7′	122°54.1′	1149	8.0

Table 3.—Trawl fishing conducted on R/V *David Starr Jordan*, September and December 1985.

Cruise and sta.	Date (1985)	Lat. (N)	Long. (W)	Start fishing	Fishing time	Depth (fm)
Cruise DS85-10(193)						
1	9-20	33°14.0′	118°58.7′	1034h	1.5h	610
2	9-21	33°02.6′	119°21.7′	0812	2.5	600
3	9-22	33°50.7′	119°26.6′	0806	1.5	690
4	9-23	35°06.3′	121°38.9′	0820	2.5	675
5	9-23	35°07.6′	121°42.1′	1256	1.5	725
6	9-24	35°06.1′	121°37.9′	0856	1.5	615
7	9-24	35°10.0′	121°38.1′	1301	1.5	550
8	9-25	34°33.4′	121°08.2′	1320	1.5	500
Cruise DS85-12(195)						
9	12-5	34°53.4′	121°34.5′	1138	1.5	600
10	12-5	34°58.5′	121°35.9′	1623	1.5	650
11	12-6	35°10.7′	121°42.3′	1115	1.5	685
12	12-7	35°44.6′	122°03.8′	1008	1.5	635
13	12-7	35°53.1′	121°56.3′	1520	1.5	700
14	12-8	36°13.2′	122°13.4′	0811	1.5	570
15	12-8	36°15.3′	122°22.9′	1410	1.5	760

subspecies, *C. armatus variabilis*.

This report deals primarily with aspects that pertain to the harvest and utilization of the Pacific grenadier, providing information on fishing methods, catch rates, distribution, and qualities of its flesh. Information on its biology is also included as well as data on giant grenadier and sablefish, *Anoplopoma fimbria*, which are often caught together with Pacific grenadier.

Materials and Methods

Data Sources

Fishing data provided in this report were obtained from several sources. A large part came from free-vehicle longline (hook and line) fishing conducted by Scripps Institution of Oceanography (SIO), mainly by Carl Hubbs in 1965, 1967, and 1971 and from cruises sponsored by the SIO Marine Life Research Group (MLRG) primarily during 1971 and 1972 (Table 1). Plankton samples from the surface to near bottom depths were also collected on the MLRG cruises. More recent data were gathered during two National Marine Fisheries Service (NMFS) research cruises in September and December 1985 on the NOAA research vessel *David Starr Jordan*. On these NOAA cruises, both bottom trawl and longline gear were used to catch grenadiers and other species in deep water (Tables 2, 3).

Our study area included offshore waters north of Cedros Island to Cape Mendocino but mainly near San Diego to Monterey, Calif. (Fig. 4). Fish taken south of Pt. Conception were predominantly caught on free-vehicle longlines. Longline sets included here (Tables 1, 2) were conducted at depths of 153-1,624 fm (280-2,970 m). Trawl tows are from the *Jordan* cruises in depths of 500 to 760 fm (915-1,391 m; Table 3). Maximum trawling depth was limited by the length of cable available on the *Jordan*.

Hook and Line Methods: Free-Vehicle Longline

In free-vehicle sampling, the gear or instrument package is allowed to free-fall to the sampling depth untethered to the ship. The package, which includes floats, returns to the surface after expendable weights are disengaged. The principal components of a free-vehicle longline are: 1) A main line with hooks attached and sufficient flotation to maintain positive buoyancy after the weight is released; 2) a locating float outfitted with a mast bearing a prominent flag, and as needed, other aids for locating the gear such as a radio transmitter or a strobe light; and 3) a chemical, electrical, mechanical, or sonic device which separates the disposable weight from the rest of the gear to allow the longline to return to the surface (Phleger and Soutar, 1971; Shutts, 1975). Size of gear, sampling depth, required precision of release time, and monetary costs are important considerations in choice of free-vehicle equipment.

Figure 5 illustrates a free-vehicle longline used on the *Jordan* and some of the SIO cruises. Each 19 l (5-gallon) plastic carboy, used for floatation and filled with Isopar M, an industrial solvent[2], provides about 4.5 kg (10 pounds) of flotation (Shutts, 1975). Both SIO and NMFS longlines were designed to fish vertically with a weight on the bottom of the longline and floats at the top. On each longline, from 25 to 100 hooks were spaced 1 m (39 inches) apart and baited with cut squid. The bottom hook was usually situated about 1.8 m (6 feet) off the bottom. Long-shank Mustad-Best Kirby hooks, size 8/0, were used on most SIO longline sets. On a few early SIO, as well as on most NMFS longline sets, equal numbers of these hooks were used together with size 6 or 9 Mustad tuna circle hooks. As catch results of the long-shank hooks appeared to be somewhat higher, the use of tuna circle hooks was discontinued in later SIO longline sets.

Most SIO longlines and all of those used on NMFS cruises were equipped with magnesium link release devices. Magnesium undergoes electrochemical corrosion in sea water when in contact with electron acceptors such as iron or zinc (Van Dorn, 1953; Isaacs and Schick, 1960). When the magnesium link disintegrates, the weight is detached and the rest of the gear rises to the surface. Soak time of the fishing gear was varied by using magnesium rods that were machined to specific diameters or by using "off-the-shelf" magnesium welding rods of various diameters. For precise release time, an electronically timed magnetic release mechanism[3] was also used on some of the SIO longline cruises. Two of the simpler release mechanisms made with magnesium welding rods are

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[2] Isopar M, a solvent with a relatively high flash point, is manufactured by Humble Oil Refining Co. Mention of trade names or commercial firms does not imply endorsement by Scripps Institution of Oceanography or the National Marine Fisheries Service, NOAA.

[3] Daniel Brown, c/o MLRG, Scripps Institution of Oceanography, La Jolla, CA 92093. Unpubl. manuscr.

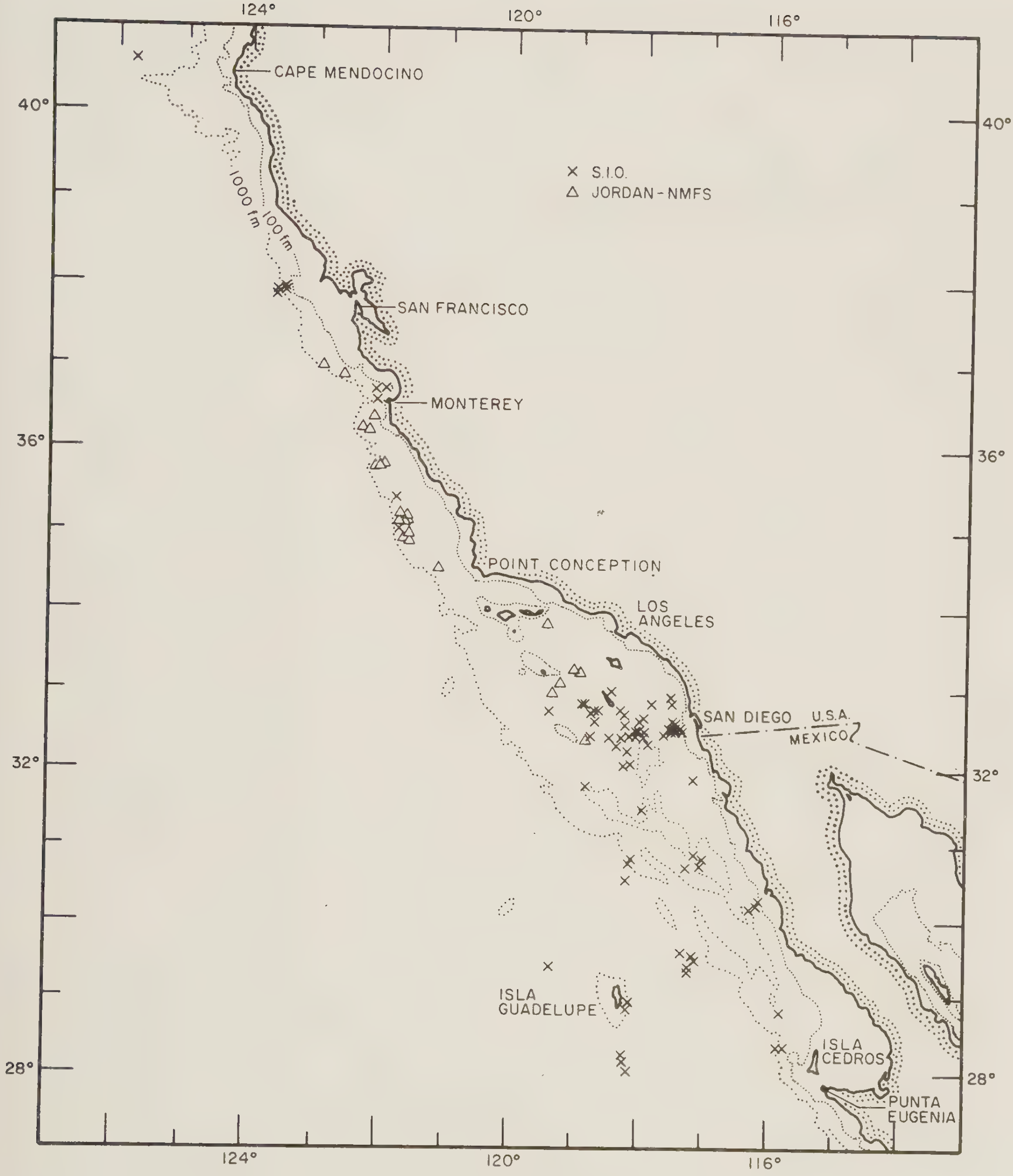
124°
120°
116°
40°
36°
32°
28°
CAPE MENDOCINO
1000 fm
100 fm
× S.I.O.
△ JORDAN-NMFS
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
LOS ANGELES
SAN DIEGO
U.S.A.
MEXICO
ISLA GUADELUPE
ISLA CEDROS
PUNTA EUGENIA

Figure 4.—Sites of fishing conducted on SIO and NMFS cruises.

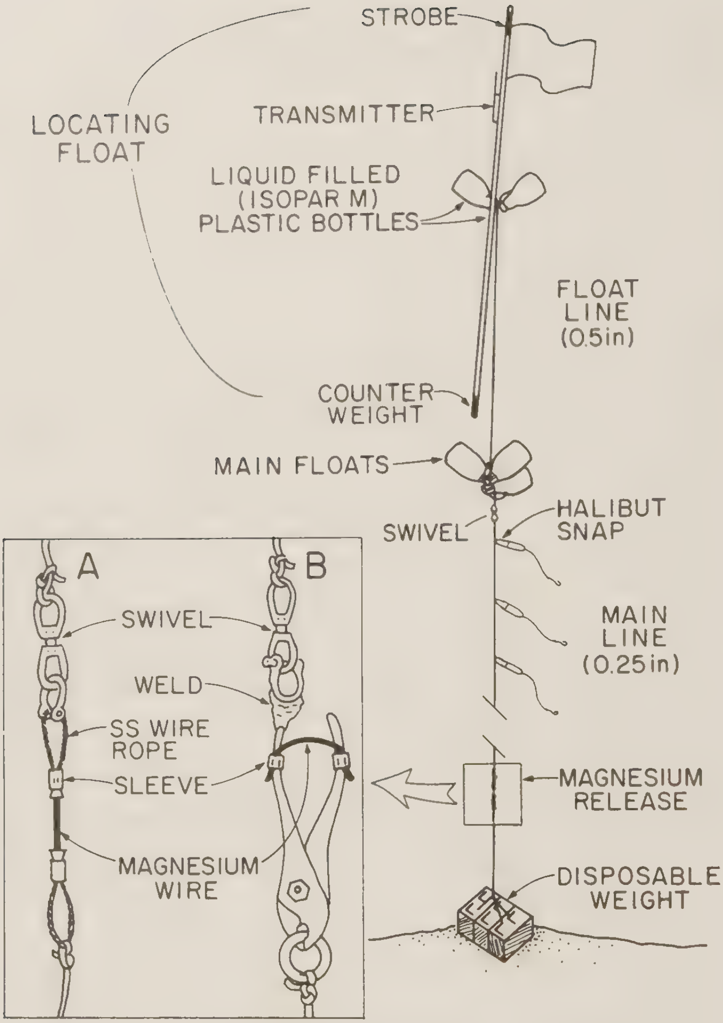

Figure 5.—Free-vehicle longline gear used to catch grenadiers in deep water. The type A release mechanism was developed by D. Brown (personal commun.) and type B by A. Soutar (Phleger and Soutar, 1974).

illustrated in the Figure 5 inset. The type shown in Figure 5A was constructed by simply crimping wire loops on a magnesium welding rod. Unlike other release devices used during SIO cruises, this type of linkage causes the magnesium rod to receive direct strain from the floats and the weight, resulting in shorter and more unpredictable release times than if no strain were present. Although unsophisticated, it gave good results on the NMFS cruises. Longlines using this device with a 2.3 mm (0.09 inch) diameter magnesium wire resurfaced after 6.1-8.2 hours in 5 trials in September 1985 and 7.6-9.0 hours in 6 trials in December 1985. On most SIO-MLRG cruises we used a modified version of the plier-release magnesium link gear described by Phleger and Souter (1971) (Fig. 5B). The strain between the weight and floats is taken up by the plier, resulting in a more predictable and consistent release time.

The research vessel was usually deployed near the setting site about 1-2 hours before the estimated time of resurfacing of the gear. The free-vehicle longline invariably resurfaced close to the drop site, but drifted away with the wind and currents at the surface. When the catch was not recovered promptly we experienced problems of predation by birds, sharks, and sea lions.

Soak time is the period of time from the disappearance below the surface of the mast when setting the longline to when the gear was again detected on the surface, through visual sighting or audible signal. We estimate that the time the gear was on the bottom, in fishing position, was about an hour less than total soak time when fishing at 500-700 fm (914-1,280 m). In a single test with a time-depth recorder, the gear took 30 minutes to sink to the bottom at 680 fm (1,244 m). Using a magnetic-release device with precise timing we obtained a rise time of 32-39 minutes from depths of 500-710 fm (915-1,299 m). The surprisingly constant rise times may have resulted from the relatively faster rise rate of the deeper sets which caught more grenadiers, which have gas bladders which expand to provide more buoyancy as the gear rises, than sablefish, which do not possess gas bladders. In shallower sets the reverse was true as more sablefish than grenadiers were caught.

Bottom Trawling

The trawl used in 1985 aboard the *David Starr Jordan* was a standard high-rise bottom trawl, designed to catch rockfish, *Sebastes* spp. The webbing was made of polypropylene twine throughout, with a stretched mesh of 114 mm (4.5 inches). The cod end had an inner liner of 12.7 mm (0.5-inch) mesh webbing. The headrope, 23 m (75 feet) long, and the footrope, 34 m (110 feet) long, were constructed of rope-wrapped wire cable and 76 mm (3 inches) rubber discs. Trawl doors were standard V-doors, 1.5 × 2.1 m (5 × 7 feet) constructed of metal frames and wood sidings. Trawl cable diameter on the *Jordan* was 16 mm (5/8 inches), and each of two winches held 1,100 fm (2,000 m) of cable. The cable-to-depth ratio varied from 1.2:1 for deep tows, to 2:1 for shallower tows. All available cable was used for tows deeper than 650 fm (1,200 m).

All trawl tows were made in daylight hours. Tow sites were selected primarily on the basis of depth and no attempt was made to sample the study area systematically. Tow duration was 1.5 hours, starting from the time the trawl cable had been completely payed out. Towing speed was about 2 knots.

Plankton Sampling for Eggs and Larvae

Plankton was sampled during SIO-MLRG cruises using modified 1 m CalCOFI nets (Brinton, 1967), 2 m Stramin net (Wimpenny, 1966), and 3 m Isaacs-Kidd midwater trawl (IKMT) (Isaacs and Kidd, 1953). The nets were towed obliquely to sample the entire water column, with the ship underway at speeds of 1-2 knots for the CalCOFI net and IKMT, and 2-3 knots for the Stramin net. The CalCOFI nets were used in series of four nets that were opened and closed by messengers to collect discrete samples from different depths. The nets had wide collars to accommodate pursing lines to close the nets, and were towed from modified Leavitt (1938) release mechanisms. The system was essentially the same as that used by Brinton (1967). The nets, which were made with synthetic Nytex webbing with 0.3 or 0.5 mm mesh, were towed open for about an hour. Two or three series of these nets were spaced to cover the entire water column, but the coverage was uneven due to malfunction of some of the nets. Flowmeters attached to each net recorded the amount of water sampled by the net, and some of these meters were also capable of recording the depth sampled as well. A 408 kg (900 lb) lead weight was attached to the end of the cable to minimize the wire angle. These tows were taken at depths of about 400-1000 fm (732-1,829 m) on 9 cruises made in February, April, August, September, and December of 1971, February and April 1972, and March and May 1973. Open-net tows with the Stramin net and IKMT were also taken on these cruises in the same area. Stramin net tows were made on cruises of June, August, September, November, and December of 1971, and February and April 1972; and IKMT tows (in the same area but only at 600-680 fm depths) in February 1972, and March and May 1973. The Stramin net was lowered until it was near bottom, then hauled to the surface in tows that lasted 1.5-4 hours. Each IKMT station consisted of three tows using different towing wire lengths, designed to cover the entire area from near bottom to the surface. Each tow lasted 2-3 hours. The net used on the IKMT was entirely of 0.5 mm mesh Nytex netting. The Stramin net was made of 1 mm mesh Stramin netting. An acoustical pinging device monitored the approximate depth of the nets, and a Benthos time-depth recorder (model 1170) was attached to the net frame or near the distal end of the cable to record depth and time data for all plankton tows.

Data Collection and Analysis

All Pacific grenadiers caught on hook and line, and subsamples of those caught in trawls were measured, and some were weighed and sexed as well. Length measurements taken were: 1) Total length (TL; snout to tip of intact tail); 2) anal length (SVL; snout to vent); and 3) head length (HL; snout to posterior edge of gillcover). The tips of the tail of many individuals showed evidence of undergoing regenerative growth after having been severed, or were missing owing to injury during capture. These fish were excluded from length statistics reported in this paper.

Sacular otoliths were obtained from Pacific grenadier for age determination. To better differentiate the calcified bands, the otoliths were studied by the "break and burn" method (Chilton and Beamish, 1982), being split and exposed to a flame before being examined with the aid of a microscope. A FISHPARM subroutine (Saila et al., 1988) was used to generate a growth curve from estimated ages (otolith band counts) and anal lengths of 60 *C. acrolepis* of both sexes. We combined these data because of the small sample size and because of the lack of age-at-length data by sex. The subroutine fits the von Bertalanffy (1938) equation:

$$l_t = L_\infty \{1 - \exp(-K[t - t_o])\}$$

where l_t is anal length at time t, L_∞ is the asymptotic length, K is the growth coefficient, and t_o is the time when length would theoretically be zero.

Gonads were removed and preserved in 10 percent Formalin, and sexes were recorded for most fish caught on MLRG-SIO cruises. The material was examined later in the laboratory, and all female fish were classified as to state of maturity (immature, ripening, or spent). Ovaries collected from 28 fish caught during February, March, April, November, and December 1974 were examined to get egg counts during different stages of development. Subsamples weighing between 0.003 and 0.035 g each were taken from the anterior and posterior parts of each ovary. The ovarian tissue was treated with several drops of methylene blue solution, then flushed with water. Eggs were counted and measured and classified into the following groups:

Stage 0: Eggs nearly completely stained and measuring 0.05-0.20 mm diameter.

Stage 1: Eggs only stained on the outer half and measuring 0.20-0.28 mm.

Stage 2: Eggs unstained or only lightly stained on the outer surface and measuring 0.28-0.80 mm.

Stage 3: Eggs unstained or only lightly stained on the outer surface and measuring 0.80-1.6 mm.

Our stages 2 and 3 correspond to those used by Stein and Pearcy (1982). We found no ripe eggs that they classified as stage 4. The outer membrane of the ovaries was removed and excluded from the weight of the ovaries in our calculations.

The relationship of various body measurements to total length was calculated to allow comparison with the work of others because the long, slender, and fragile tail of *C. acrolepis* was often damaged. The relationships of anal length to weight and total length to weight

Table 4.—Catch data (listed by depth) from SIO free-vehicle longline stations recorded in Table 1. Total catch includes fish other than Pacific grenadier and sablefish.

Cruise and station	Depth (fm)	No. of hooks	Pacific grenadier		Sablefish		Total catch per hook
			Catch	No./hook	Catch	No./hook	
MV71-I-49	153	25	0	0	13	0.52	0.64
MV71-2	240	25	0	0	6	0.24	0.24
MV71-I-46	293	25	0	0	9	0.36	0.40
MV71-I-50	304	25	0	0	20	0.80	0.80
MV71-I-57	310	25	0	0	15	0.60	0.60
MV71-I-40	320	25	0	0	7	0.28	0.28
MV71-2	330	25	0	0	11	0.44	0.44
MV65-III-18	337	30	0	0	6	0.20	0.20
MV71-I-52	346	25	0	0	17	0.68	0.68
M6-3	400	50	0	0	23	0.46	0.46
MV67-II-26	400	30	0	0	25	0.83	0.83
SC2-74	420	100	0	0	35	0.35	0.35
MV65-II-33	426	30	0	0	10	0.33	0.33
M1-2	445	100	0	0	32	0.32	0.32
M5-3	445	50	0	0	14	0.28	0.28
M3-3	445	100	0	0	23	0.23	0.23
MV71-I-24	453	26	0	0	10	0.38	0.38
MV67-IA-22	455	30	0	0	0	0	0.03
MV71-I-16	490	26	3	0.12	0	0	0.12
M10-5	530	50	1	0.02	30	0.60	0.62
MV67-IA-28	536	30	4	0.13	0	0	0.17
MV65-III-24	537	30	2	0.07	10	0.33	0.40
S2-2	550	100	2	0.02	10	0.10	0.12
M10-6	550	50	5	0.10	17	0.34	0.44
MV65-III-34	555	30	1	0.03	18	0.60	0.63
M9-3	555	50	7	0.14	19	0.38	0.54
MV71-I-58	560	25	9	0.36	8	0.32	0.68
MV67-II-15	560	30	12	0.40	9	0.30	0.70
M8-2	561	50	12	0.24	13	0.26	0.50
MV71-I-51	563	25	12	0.48	2	0.08	0.56
M12-2	568	50	15	0.30	18	0.36	0.66
M9-4	595	50	5	0.10	12	0.24	0.34
M15-5	600	69	13	0.19	8	0.12	0.30
M8-3	605	50	15	0.30	11	0.22	0.52
MV65-III-35	610	30	6	0.20	5	0.17	0.37
M12-3	610	50	19	0.38	20	0.40	0.78
SC74	610	100	43	0.43	6	0.06	0.49
M11-2	620	50	11	0.22	10	0.20	0.44
SC79	620	50	6	0.12	1	0.02	0.14
SC3-74	630	50	15	0.30	16	0.32	0.62
M8-4	630	50	10	0.20	19	0.38	0.58
MV65-III-36	631	30	3	0.10	15	0.50	0.60
M11-4	647	93	7	0.08	3	0.03	0.11
70RI-7	655	25	11	0.44	6	0.24	0.68
MV71-I-17	655	26	13	0.50	0	0	0.50
70RI-8	656	25	7	0.28	5	0.20	0.48
SC17	660	99	5	0.05	0	0	0.05
MV71-I-4	663	25	8	0.32	3	0.12	0.44
M15-3	668	100	21	0.21	7	0.07	0.28
M15-1	670	100	22	0.22	4	0.04	0.26
M8-6	670	50	21	0.42	1	0.02	0.44
70RI-2	680	25	11	0.44	5	0.20	0.64
70RI-3	680	25	11	0.44	5	0.20	0.64
70RI-4	680	25	6	0.24	0	0	0.28
71RI-1	680	100	40	0.40	24	0.24	0.64
M4-1	680	100	54	0.54	8	0.08	0.62
M4-2	680	50	30	0.60	4	0.08	0.68
M5-1	680	100	14	0.14	1	0.01	0.15
M6-1	680	57	26	0.46	13	0.23	0.68
M7-1	680	50	19	0.38	9	0.18	0.56
M9-1	680	50	15	0.30	11	0.22	0.52
M9-2	680	50	19	0.38	13	0.26	0.64
M10-2	680	50	22	0.44	14	0.28	0.72
M10-4	680	50	7	0.14	15	0.30	0.44
M11-3	680	49	16	0.33	4	0.08	0.41
M12-1	680	100	36	0.36	18	0.18	0.54
M13-1	680	200	53	0.26	22	0.11	0.38
MV67-IA-3	690	30	17	0.57	4	0.13	0.70
SC75	700	50	14	0.28	1	0.02	0.30
MV71-I-47	702	25	11	0.44	2	0.08	0.52
MV71-I-11	710	40	12	0.30	0	0	0.30
S2-1-1	710	100	17	0.17	1	0.01	0.19
MV65-III-37	712	30	12	0.40	4	0.13	0.57
MV71-I-10	715	40	14	0.35	0	0	0.42
M2A1	730	100	54	0.54	2	0.02	0.56
M2A2	730	50	33	0.66	1	0.02	0.68
71RI-2	735	50	4	0.08	4	.08	0.20
MV65-III-19	738	30	11	0.37	0	0	0.40
MV65-III-26	748	30	10	0.33	5	0.17	0.57
MV71-I-3	750	41	18	0.44	0	0	0.56
MV71-I-59	765	25	18	0.72	0	0	0.72
MV67-III-16	790	30	17	0.57	1	0.03	0.60
MV65-III-3	790	30	3	0.10	0	0	0.10
MV65-III-38	798	30	8	0.27	1	0.03	0.33
MV67-II-28	800	30	9	0.30	1	0.03	0.40
MV65-I-5	814	100	18	0.18	0	0	0.19
M8-7	850	50	27	0.54	1	0.02	0.62
MV67-1A-9	873	30	17	0.57	0	0	0.57
MV71-I-25	875	26	14	0.54	1	0.04	0.62
MV67-IA-7	890	30	9	0.30	0	0	0.30
MV65-III-28	896	30	7	0.23	2	0.07	0.30
MV67-IA-18	900	30	9	0.30	0	0	0.30
MV65-III-29	916	30	6	0.20	7	0.23	0.43
M1-3	925	100	54	0.54	0	0	0.54
M3-2	925	100	15	0.15	0	0	0.15
M5-2	925	50	26	0.52	0	0	0.52
M8-5	930	50	27	0.54	0	0	0.54
M6-2	937	50	27	0.54	0	0	0.54
MV71-I-42	938	25	14	0.56	0	0	0.56
MV65-III-21	952	30	10	0.33	0	0	0.40
M7-3	980	50	37	0.74	0	0	0.74
MV71-I-48	998	25	11	0.44	0	0	0.44
MV65-III-4	1017	30	3	0.10	0	0	0.18
MV67-IA-20	1024	30	0	0	0	0	0
MV71-I-60	1026	25	14	0.31	0	0	0.38
MV71-I-4	1026	39	4	0.10	0	0	0.18
MV71-I-12	1039	39	7	0.18	0	0	0.36
MV71-I-19	1050	25	10	0.40	0	0	0.44
MV67-IA-10	1075	30	8	0.27	0	0	0.37
MV71-I-26	1095	26	8	0.31	0	0	0.38
MV67-II-18	1200	30	3	0.10	0	0	0.10
MV67-IA-11	1208	30	11	0.36	0	0	0.43
MV67-II-29	1233	30	5	0.17	0	0	0.20
MV67-IA-16	1382	30	0	0	0	0	0
MV65-III-6	1391	30	0	0	0	0	0.03
MV67-II-30	1480	30	2	0.07	0	0	0.07
SIO66-50	1624	30	1	0.03	0	0	0.10

were computed using the allometric growth equation subroutine of FISHPARM (Saila et al., 1988), which fits the equation:

$$W = aL^b$$

where W is weight (kg) and L is total or anal length (mm), and a and b are constants. The relationship of anal length to total length was determined by using a least square fit of the single linear equation:

$$Y = bx + a$$

where Y is total length and x is anal length.

To investigate the market potential of grenadier flesh, samples of fillet kept on ice were sent to the Utilization Research Division (URD) of the NMFS Northwest Fisheries Science Center (NWFSC), Seattle, Wash., for chemical and taste tests. A "sensory analysis panel" composed of trained URD personnel conducted tests to classify general characteristics of the cooked flesh of both Pacific and giant grenadiers.

Fishing Results

Free-vehicle Longline

Vertically set longline gear deployed

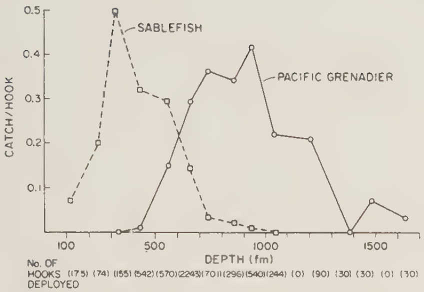

Figure 6.—SIO catch records of sablefish and Pacific grenadier by 117 free-vehicle longlines, 1965-79. Plotted points represent mean values at 100-fm depth intervals, with the number of deployed hooks representing each point in parentheses.

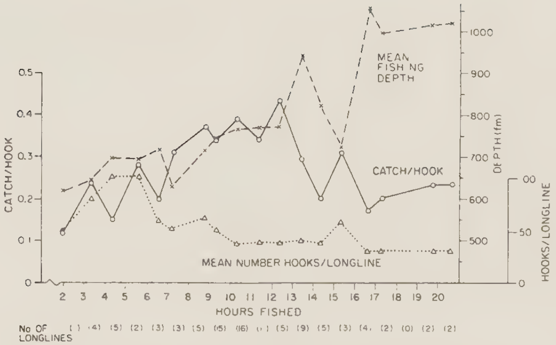

Figure 7.—Relationship of hours fished to average catch per hook, depth of fishing, and hooks per set. Data are from 97 SIO free-vehicle longlines from stations over 500 fm depth. Number of longlines are in parenthesis.

Table 5.—Catch data from longline fishing conducted on R/V *David Starr Jordan*, September and December 1985.

Cruise and station	Depth (fm)	No. of hooks	Pacific grenadier Total catch	Pacific grenadier Per hook	Sablefish Total catch	Sablefish Per hook	Total catch per hook
Cruise DS 85-10(193)							
1	695	48	0	0	1	0.02	0.02
2	626	48	5	0.10	5	0.10	0.21
3	888	48	3	0.06	3	0.06	0.12
4	835	47	12	0.26	0	0.0	0.26
5	725	48	25	0.52	0	0.0	0.52
Cruise DS 85-12(195)							
6	611	49	19	0.39	4	0.08	0.47
7	903	47	11	0.23	0	0.0	0.23
8	994	48	1	0.02	0	0.0	0.02
9	784	46	15	0.33	1	0.02	0.35
10	490	46	0	0	6	0.13	0.13
11	805	43	19	0.44	4	0.09	0.53
Total		518	110	0.21	24	0.05	0.26

Table 6.—Comparison of catch of Pacific grenadier on 25-, 50-, and 100-hook longlines listed in Table 4 from depths >500 fm. Actual number of hooks of the 25-hook group varied more than the others and averaged 28.4 hooks per longline.

Item	25-hook	50-hook	100-hook	Total
No. of longlines	47	35	15	97
No. of hooks deployed	1,328	1,724	1,492	4,544
Total catch	394	559	402	1,355
Hours fished	608.21	341.79	106.38	1,056.38
Avg. hours fished	12.94	9.76	7.09	10.89
Avg. catch per hook	0.297	0.324	0.269	0.298
Avg. catch per hour	0.648	1.64	3.78	1.28

at depths of 100-1,600 fm (183-2,926 m) in the sampling area (Fig. 4) caught mostly two species, Pacific grenadier and sablefish. Other species, which together made up less than 5 percent of the catch, were giant grenadier, abyssal grenadier, California slickhead, *Alepocephalus tenebrosus*, and finescale codling, *Antimora microlepis*. Longlines rarely failed to catch either sablefish or Pacific grenadier at these depths, confirming the ubiquitousness of these species over these waters.

Catch data from 117 free-vehicle longline sets made on SIO cruises are shown in Table 4. Longline catches made on the *Jordan* are given in Table 5. Listed are catches of Pacific grenadier and sablefish, whose depth distributions overlap considerably. Sablefish were taken from 153 to 916 fm (280-1,675 m) and Pacific grenadier from 490 to 1,624 fm (897-2,972 m). Sablefish dominated the catches from 200 to 600 fm (366-1,098 m), while Pacific grenadier was most abundant at the deeper stations, especially between 600 and 1000 fm (1,098 and 1,830 m) (Fig. 6, Table 4).

Depth readings given above refer to depths to the sea floor, but both Pacific grenadier and sablefish were caught along the entire length of the vertical longline, from the lowest to the highest hooks (about 55 fm or 100 m above the sea floor). Two longline sets with baited hooks placed well off the bottom (lowest hook at 50 m or 27 fm above the bottom at station M2A2, and 25 m or 14 fm at station M4-2) produced catch rates of 0.66 and 0.30 Pacific grenadiers per hook, respectively. This shows that the fish can find bait quite high in the water column even when there is no bait near the bottom to guide the fish.

The catch rate of 97 longline sets made in depths greater than 500 fm (915 m) (Table 6) averaged 0.30 Pacific grenadiers per hook. Differences were relatively small between 25-hook (0.30 per hook average), 50-hook (0.32), and 100-hook (0.27) longlines. From these results, expectations were for hourly catch rates to increase on average nearly in proportion to the number of hooks deployed. The somewhat lower catch of 0.65 grenadiers per hour for the 25-hook sets, compared with 1.6 per hour for 50-hook sets and 3.8 per hour for 100-hook sets (Table 6), was probably due to the disproportionate number of these sets being made in depths (Table 4) near the deep end of the species' range. Averages of 97 longline catches plotted in Figure 7 show a trend of increasing fishing time and

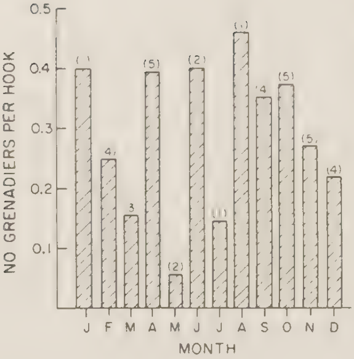

Figure 8.—Average catch rates of Pacific grenadier by free-vehicle longline, by month of fishing off southern California. Data are from SIO-MLRG fishing stations deeper than 550 fm. Number of fishing trials are in parentheses.

Table 7.—Catch (in pounds) of the most common species of fish caught per 1.5-hour tow by trawl fishing on the R/V *David Starr Jordan*. Station numbers correspond to those given in Table 3.

Station	Depth (fm)	Pacific grenadier	Giant grenadier	Sablefish	Dover sole	Channel rockfish	Total[1]
8	500	1	10	257	769	241	1,268
7	550	153	29	328	193	135	809
14	570	14	12	58	0	40	112
2	600	0	9	13	31	23	67
9	600	23	12	26	51	10	110
1	610	3	30	28	1	56	88
6	615	204	80	36	5	305	550
12	635	162	59	351	1	116	630
10	650	237	117	50	309	100	696
4	675	352	183	5	1	125	483
11	685	74	41	5	0	39	204
3	690	0	18	5	11	151	169
13	700	14	12	58	0	40	112
5	725	68	30	0	0	9	77
15	760	289	160	65	0	25	379

[1] Excluding giant grenadier, the only species presently without commercial value.

fewer hooks with increasing fishing depth. The decline in average catch per hook for longlines fished longer than 13 hours was probably also the result of fishing at deeper, less favorable depths. Catch per hook generally increased with lengths of fishing time, reaching a maximum around 8-13 hours, then declining. However, some of the highest catches were made in sets fished longer than 13 hours. For example, a catch of 0.60 fish per hook (Station M4-2 in Table 4), the second highest for Pacific grenadier, was made after 15.7 hours, and the highest catch of sablefish listed in Table 4, 0.83 per hook, (MV67-II-26) occurred when the line fished for nearly 19 hours. These results indicate that catch rates can be high with longer fishing times in productive areas. They also suggest low predation on, as well as low escapement of, hooked fish. Because sets made for longer periods were generally in very deep water, often beyond the optimum habitat of Pacific grenadier, our data probably do not reveal true catch rates after 13 hours.

Catch rates for fishing stations deeper than 500 fm (915 m) on the *Jordan* cruises (Table 5) averaged 0.21 per hook for Pacific grenadier and 0.05 for sablefish, less than the averages of 0.31 and 0.11 for the SIO cruises. The shorter average fishing time of 8.1 hours used during the *Jordan* cruises, compared with the 10.8 hours of SIO samples, may have caused the difference, but the small number of fishing stations (11) for the *Jordan* cruises also was a factor.

Figure 8, which represents the catch rate of Pacific grenadier by month, shows no clear trends in seasonal availability of Pacific grenadier off southern California. The species was available most months, though catch rates were low in several fishing trials.

Results of Trawl Fishing on R/V *David Starr Jordan*

Catches of Pacific grenadier by trawl fishing conducted on the *Jordan* are shown in Table 7. Catches of giant grenadier are included, as well as those of sablefish, Dover sole, *Microstomus pacificus*; and shortspine and longspine thornyheads, *Sebastolobus alascanus* and *S. altivelis*, respectively. The last four species are commercially valuable fishes frequently found together with Pacific grenadier. Best trawl catches of both Pacific and giant grenadiers were made in depths of 615-675 fm (1,125-1,235 m), and at the deepest trawl station, 760 fm (1,391 m). The other species were more prevalent in the shallower trawl tows, but thornyheads were also commonly caught down to 700 fm (1,281 m).

The most productive trawling locality for larger individuals of Pacific grenadier was at Santa Lucia Bank, about 50 miles northwest of Pt. Conception (Fig. 4). The area is characterized by wide expanses of flat bottom in deep water.

Plankton Sampling Results

A single 9 mm TL larval Pacific grenadier was caught in one of the CalCOFI net samples at lat. 32°31.2′N, and long. 118°05′W on 2 February 1971. The net was estimated to have sampled depths between 2.7 and 120 fm (5-220 m) from the surface over water 680 fm (1,244 m) deep. No larvae were found in the remaining 121 CalCOFI net tows made during 9 MLRG cruises, nor in twelve Stramin net samples, nor nine IKMT samples from those cruises.

Life History of the Pacific Grenadier

Distribution

Coryphaenoides acrolepis ranges from Japan and the Okhotsk and Bering Seas on the western Pacific, eastward along the Aleutian Islands to the west coast of North America (Iwamoto and Stein, 1974), as far south as Cedros Island (ca. lat. 28°N, station MV65-5, Table 1) off Baja California, Mex. It generally occurs along continental slope waters and is mainly caught with bottom sampling gear (otter trawls, bottom set hook and line). Our free-vehicle longline catches of *C. acrolepis* were made at depths ranging from 490 to 1,640 fm (896-3,000 m), the deepest capture being made at station SIO66-50. It may inhabit shallower depths at higher latitudes, as Okamura

(1970) gives a depth range for the species of 339-1,202 fm (620-2,200 m).

Numerous photographic observations have been made with remote cameras of Pacific grenadiers swimming near the bottom (Phleger, 1971). Although they are usually taken with bottom sampling gear, some adults (Iwamoto and Stein, 1974) as well as the youngest stages (Stein, 1980) have been caught in midwater. In Stein's samples, the youngest larvae were collected at depths less than 110 fm (200 m) from the surface, with larger larvae and juveniles occurring deeper in the water column. Savvatimskii (1969) similarly reported that small *C. acrolepis* of 10-15 mm (0.39-0.59 inch) TL were found at 55-110 fm (100-200 m) and we collected a 9 mm (0.35 inch) TL larva in a net which sampled 2.7-120 fm (5-220 m) below the surface off San Diego. These records indicate that the youngest Pacific grenadiers occur near surface layers. The largest juvenile reported taken in a midwater trawl by Stein and Pearcy (1982) measured 83 mm (3.3 inch) TL, and the smallest taken in bottom trawl, 73 mm (2.9 inches) TL. Thus the size at which the fish adopts a benthic habitat seems to be around 80 mm (3.1 inches) TL (Stein and Pearcy, 1982).

Reproduction

Ripe females of *C. acrolepis* have been reported off Kamchatka, eastern U.S.S.R., in September (Savvatimskii, 1969) and off Oregon in September, October, and April, with spent females also occurring in October (Stein and Pearcy, 1982). In the SIO-MLRG sampling program conducted off southern California, no females were found with a preponderance of ripe (2 mm) eggs. Oocytes of females with enlarged ovaries were in the ripening stage (0.8-1.6 mm). The number of females with ovaries at this stage was also relatively low throughout the year, but females with empty, flaccid ovaries that indicated a spent condition were common (Fig. 9). The number of spent females was especially high in spring and early summer. During this period the number of ripe males was also greater. However, spend females and those with ripening stage 3 (0.8-1.6 mm) oocytes were found throughout the year. Occurrence of these stages was lowest in August and September when many females carried dominant stage 2 (0.4-0.8 mm) oocytes.

Table 8.—Estimated egg counts of Pacific grenadiers listed by snout to vent measurements (SVL). Cruise and station data (e.g., M15-8) is given in Table 1.

Sample	SVL (mm)	Wt. (kg)	Stage 0	Stage 1	Stage 2	Stage 3
M15-8-1	162	0.45	427,662	0	0	0
M15-1-14	189	0.75	1,188,500	59,888	1,279	20,749
M16-1-18	234	1.10	1,355,458	139,772	0	0
M13-12	238		3,193,900	357,493	3,362	0
M15-6-17	239	1.30	2,218,260	124,264	18,508	68,742
SC3-74-19	241	1.10	2,772,477	243,467	6,087	0
M16-1-9	241	1.30	3,677,071	66,274	179,270	0
M16-1-8	244	1.30	2,443,828	210,883	13,730	77,434
M16-1-16	244	1.30	3,728,688	403,977	11,932	56,676
M15-1-13	244	1.25	1,466,740	110,730	63,028	0
M15-5-21	249	1.30	1,585,946	95,966	10,042	73,090
M15-7-5	249	1.30	1,666,046	92,237	52,819	61,228
M15-1-17	262	1.60	1,246,635	225,810	90,675	0
M15-7-3	262	1.65	3,513,178	537,420	166,384	70,647
M15-1-23	262	1.60	2,503,379	174,076	87,038	0
SC3-74-22	264	1.60	2,051,348	235,664	33,921	0
M16-1-12	265	1.50	1,590,299	256,262	40,073	0
SC74-4	270	1.80	3,412,846	114,168	196,225	0
M15-6-13	276	1.75	2,364,618	246,298	42,324	60,172
SC3-74-18	276	1.70	1,668,184	163,299	8,165	0
M15-1-8	286	2.10	4,212,138	612,496	156,546	107,750
M13-3	289		3,039,594	313,322	51,509	150,258
SC74-11	296	2.00	1,079,055	103,242	9,436	102,965
M15-1-12	301	2.10	5,927,000	435,821	117,645	0
M15-3-9	304	2.10	2,564,447	468,630	231,712	0
SC3-74	315	2.50	3,882,486	385,845	10,465	111,239
M15-1-18	318	2.65	7,991,482	681,650	358,280	0

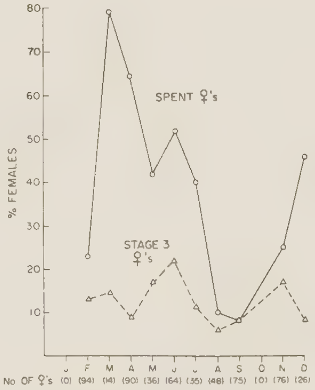

Figure 9.—Proportions of ripening and spent female Pacific grenadier making up some of the MLRG longline catches during different months of the year. Number of females are in parentheses.

Length at maturity appears to be around 650 mm (26 inches) TL for females, and about 500 mm (20 inches) TL for males. Most females with oocytes 0.8 mm and larger weighed 1.1 kg (2.4 pounds) or more and measured >650 mm (>25.6 inches) TL; the smallest was 585 mm (23 inches) TL and 0.75 kg (1.6 pounds). Stein and Pearcy (1982) found 0.8-1.6 mm eggs in individuals as small as 460 mm (18.1 inches) TL in their trawl samples. The smallest ripe male in their catches measured 485 mm (19.1 inches) TL and weighed 0.5 kg (1.1 pounds). Ripe males in our SIO-MLRG samples were always larger, but only a few individuals caught on our longlines were smaller than 500 mm (19.7 inches) TL and the smallest measured 400 mm (15.7 inches) TL.

Like other macrourids, fecundity of *C. acrolepis* is relatively high. In seven females, Stein and Pearcy (1982) estimated counts of 22,657-118,612 ($\bar{x}$ = 70,025) eggs. Our counts for 28 females are given in Table 8. Only stage 0 (0.05-0.20 mm) oocytes were present in the single immature female examined. A slightly larger female of 0.7 kg (1.6 pounds), probably just attaining maturity, had an estimated 20,749 stage 3 eggs. Highest estimated number of stage 3 oocytes was 150,258 from a female weighing around 2.0 kg (4.5 pounds).

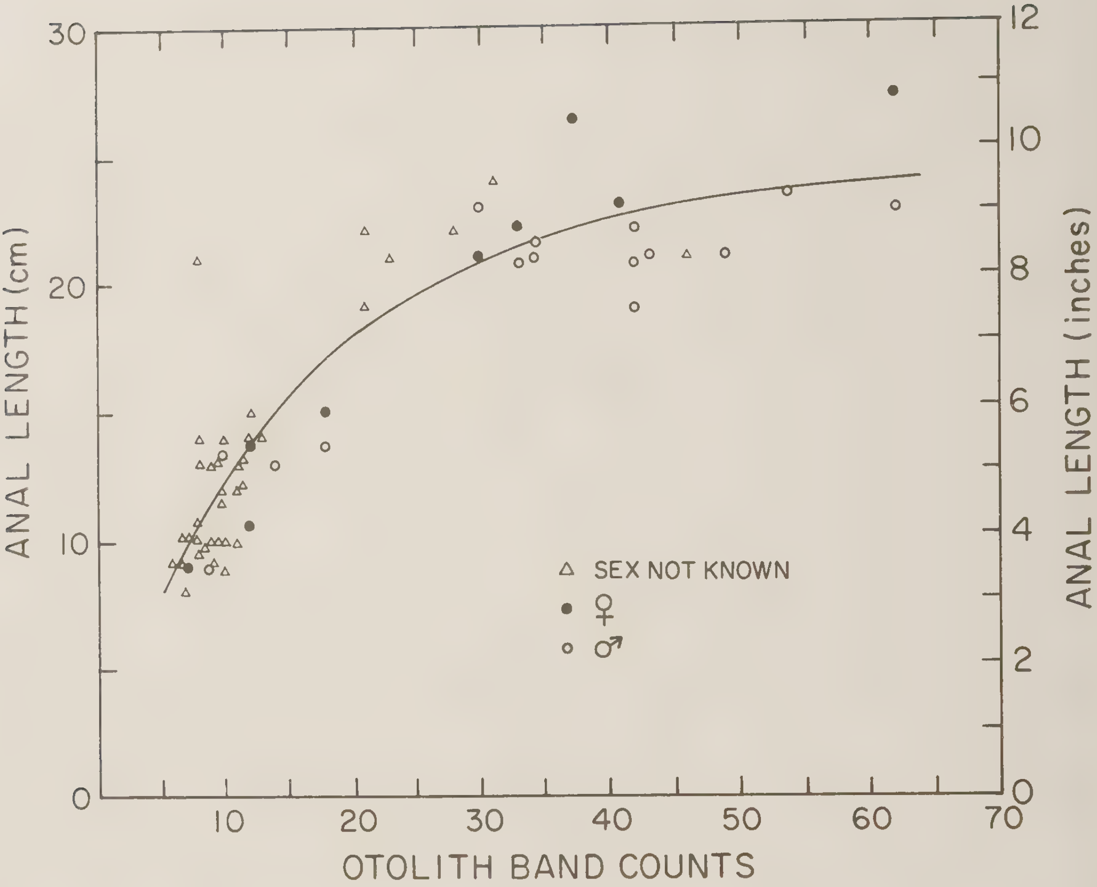

Figure 10.—A von Bertalanffy growth curve (sexes combined) and otolith ring count by size for 60 Pacific grenadiers.

The number of oocytes generally increased with fish size, but there were wide differences among individuals of similar sizes (Table 8). Stages 0 and 1 oocytes were always numerous and their numbers were independent of the developmental state of the ovaries, even in those that were spent. Nearly all oocytes found in spent females were in these stages. The presence of large numbers of stage 2 oocytes together with dominant stage 3 oocytes in some ovaries raise some questions as to the fate of the former. One can speculate a second spawning or perhaps these eggs are resorbed.

Despite the apparently high fecundity, the young of *C. acrolepis* have rarely been found. After sorting through 2,700 midwater trawls taken off Oregon, Stein (1980) found only 78 larvae and juveniles of *C. acrolepis*.

Age and Growth

Rings were found on sacular otoliths but the lines were obscure in large individuals, especially near the periphery of the otolith. We also had difficulty in reading the calcified bands in some of the otoliths from larger fish because of irregular patterns of band deposition. Even so, the data fitted the von Bertalanffy curve rather well (Fig. 10), with much of the variability about the mean explained by the least squares predictor ($R^2 = 0.82$). The growth equation for estimated ages 6-62 for both sexes was found to be represented by

$$l_t = 24.24\{1 - \exp(-0.063[t - 1.093])\}$$

The growth curve assumes that the otolith rings represent annual growth marks, but we emphasize that we have no confirmation that this is true. Kulikova (1957, in Gordon, 1979), using rings on scales, reported a rapid growth rate for

Pacific grenadier, but Brothers et al. (1976) using sacular otoliths suggested the opposite, estimating a 58 cm (22.8-inch) individual to be 10-11 years old. As in our study, the rings were presumed to represent annual growth rings, but this has yet to be confirmed (Wilson, 1982). Our growth curve for Pacific grenadier shows a considerably slower growth rate than does Kulikova (1957), but somewhat faster than that found by Brothers et al. (1976). Known values for females in Figure 10 indicate a faster growth rate for females. Unfortunately sex records of a number of individuals are lacking, and the growth curve in Figure 10 represents all otoliths examined.

The length-weight relationships computed for 141 males and 156 females, all with intact tails (Fig. 11), were as follows:

Females

$$Wt = 8.879 \times 10^{-7} AL^{2.579} \quad R^2 = 0.92$$

$$Wt = 6.889 \times 10^{-9} TL^{2.922} \quad R^2 = 0.90$$

Males

$$Wt = 5.107 \times 10^{-6} AL^{2.251} \quad R^2 = 0.81$$

$$Wt = 2.225 \times 10^{-8} TL^{2.725} \quad R^2 = 0.87$$

where Wt is weight (kg), AL is anal length (mm), and TL is total length (mm).

The relationship of total length to anal length is given in Figure 12. A least squares fit gave the following equations:

Males

$$Y = 2.308x + 122.158 \qquad R^2 = 0.864 \quad P<0.0001$$

Females

$$Y = 2.276x + 115.4 \qquad R^2 = 0.925 \quad P<0.0001$$

where Y is total length and x is anal length.

Food and Feeding

Because of expansion of their gas bladders, the stomachs of grenadiers are usually everted when they are captured near the bottom and hauled to the surface. Information on food habits of *C. acrolepis*, which has a large gas bladder, is thus scarce. Pearcy and Ambler (1974) found several species of cephalopods and crustaceans and remains of amphipods and fish in a few noneverted stomachs. Okamura (1970) lists as food items squid (37 percent), euphausiids (24 percent), fish (20 percent), and prawns (19 percent). Pacific grenadier has been collected thousands of meters above the sea floor and is considered by some to be bathypelagic rather than benthic. Savvatimskii (1969) found indications that it fed on nekton and macroplankton. Several squid beaks were found by one of us in an experimental fish trap (Brown, 1975) that had caught a Pacific grenadier near the sea floor. The beaks were presumed to have been regurgitated by the fish. In the SIO stomach samples we found remains of fish, euphausiids, other crustacea, squid beaks, and in the intestines, items such as polychaetes and sponge spicules, suggesting a generalized diet which included fish, plankton, and bottom organisms. The number of intact stomach samples we were able to obtain were too few for significant analysis, however.

Flesh Characteristics

Because its tail is thin and long, the amount of flesh obtainable from Pacific grenadier is less than that from other fish of comparable size. We obtained a fillet yield (weight of flesh compared with total weight) of only 22-26 percent ($\bar{x} = 24.3$ percent) from larger individuals. Kremsdorf et al. (1979) were able to get a greater yield of 28 percent. Skin-on carcasses, with the head and intestines and most of the tail removed, averaged 50 percent of the total weight. Proximate analyses for Pacific and giant grenadiers obtained from NWFSC Utilization Research Division and other data are given in Table 9. Protein content of giant grenadier was extremely low, and that of Pacific grenadier, 15.2 percent, was also considerably lower than the average of 19.5 percent found for 35 species of fishes, excluding sharks (Gooch et al., 1987).

Table 9.—Proximate composition (wet weight basis) for Pacific and giant grenadier.

	Pacific grenadier		Giant grenadier	
Item	Sample 1	Sample 2	Sample 1	Sample 2
Protein (%)	15.8	15.9	10.8	15.8
Fat (%)	0.1	0.2	0.2	0.2
Ash (%)	1.2	1.1	1.2	1.0
Moisture (%)	83.0	83.1	88.5	83.0
Energy (cal /100 g)	64.0	65.0	45.0	62.0
Minerals mg/g)				
Ca	148.000	111.700	180.900	175.200
Cu	0.424	0.896	0.147	0.441
Fe	3.820	4.650	3.330	3.310
K	2,748.000	3,144.000	1,368.000	3,065.000
Mg	432.000	332.000	313.000	348.000
Na	1,952.000	1,042.000	3,134.000	1,140.000
P	1,438.000	1,422.000	809.000	1,422.000
Sr	1.390	0.767	1.540	1.052
Zn	3.940	2.860	3.590	2.480

Table 10.—Characteristics of flesh and flavor profile of Pacific and giant grenadier. Scale is from 0 (none) to 7 (high). Data are from Alice Hall, NMFS, NWFSC, 2725 Montlake Blvd. E., Seattle, WA 98112.

	Pacific grenadier		Giant grenadier
Item	Sample 1	Sample 2	Sample 1
Flesh characteristics			
Darkness	1.73	0.44	0.45
Flakiness	5.09	5.44	3.36
Hardness	3.45	2.89	1.36
Chewiness	4.18	3.33	1.73
Fibrousness	4.36	3.33	2.45
Moistness	2.73	3.22	5.00
Oiliness	0.64	0.67	1.09
Flavor profile			
Flavor intensity	2.91	3.00	3.82
Sweet	1.45	2.11	0.91
Salty	2.00	1.00	3.27
Sour	0.36	0.33	0.36
Gamey	0.00	0.22	0.27
Fish oil	0.00	0.11	0.36
Shellfish	0.00	0.11	0.00
Earthy	0.53	0.51	0.30

Findings of the sensory analysis panel at NWFSC, which tested and classified flesh characteristics of both Pacific and giant grenadier, are averaged and summarized in Table 10. Among the good attributes of Pacific grenadier flesh were firm texture, agreeable white color, and nonobjectionable taste[4]. Flesh of the giant grenadier was unpalatable, according to the panelists, primarily because of its soft texture. This was reflected in the low scores for flakiness, hardness, chewiness, and fibrousness, and high score for moistness.

Discussion

Until quite recently a single species of

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[4] Alice Hall, Northwest Fisheries Science Center, NMFS, NOAA, 2725 Montlake Blvd. N.W., Seattle, WA 98112. Personal commun.

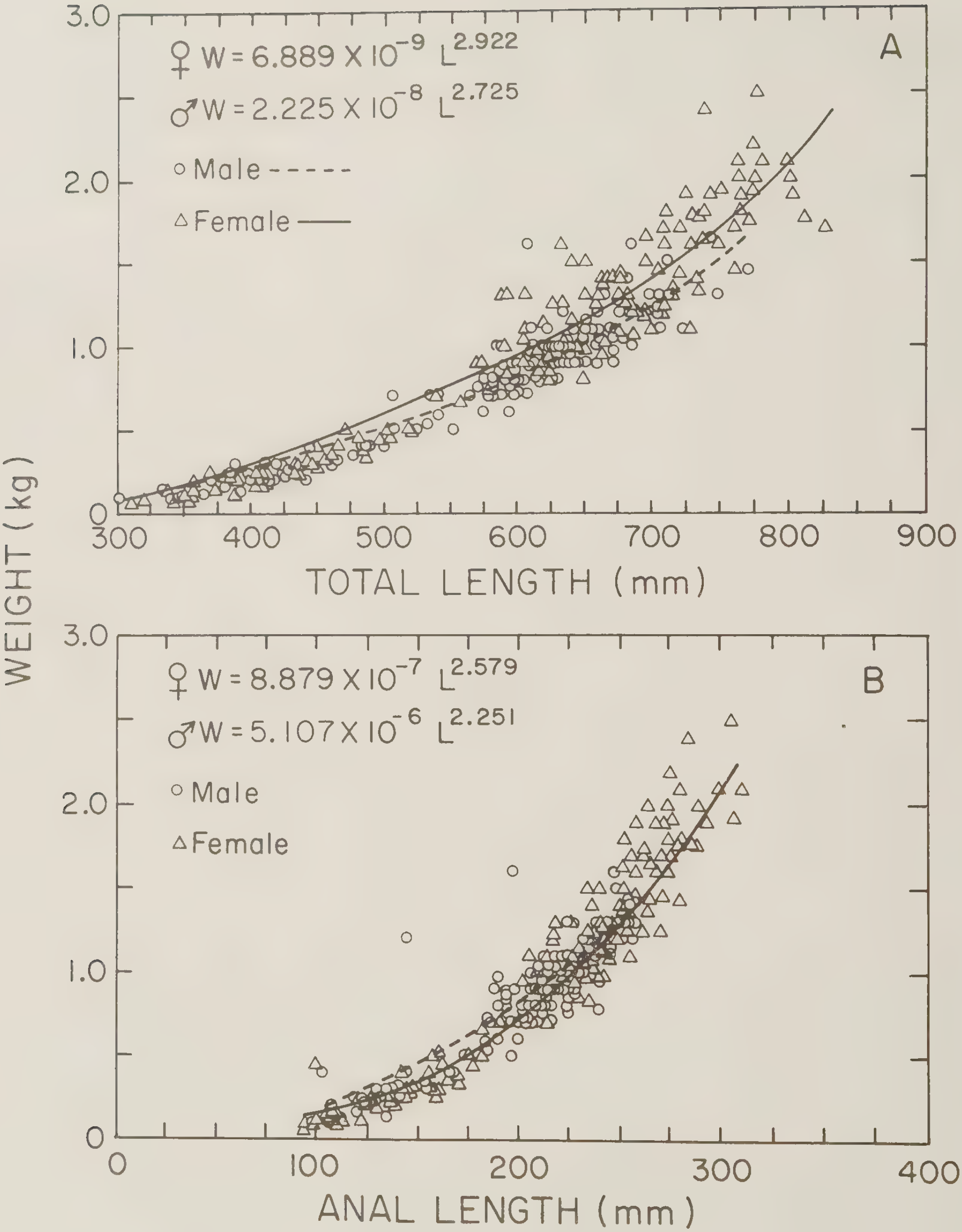

Figure 11.—Length-weight relationships of Pacific grenadier. A shows weight (kg) to total length (mm) and B illustrates weight to anal length.

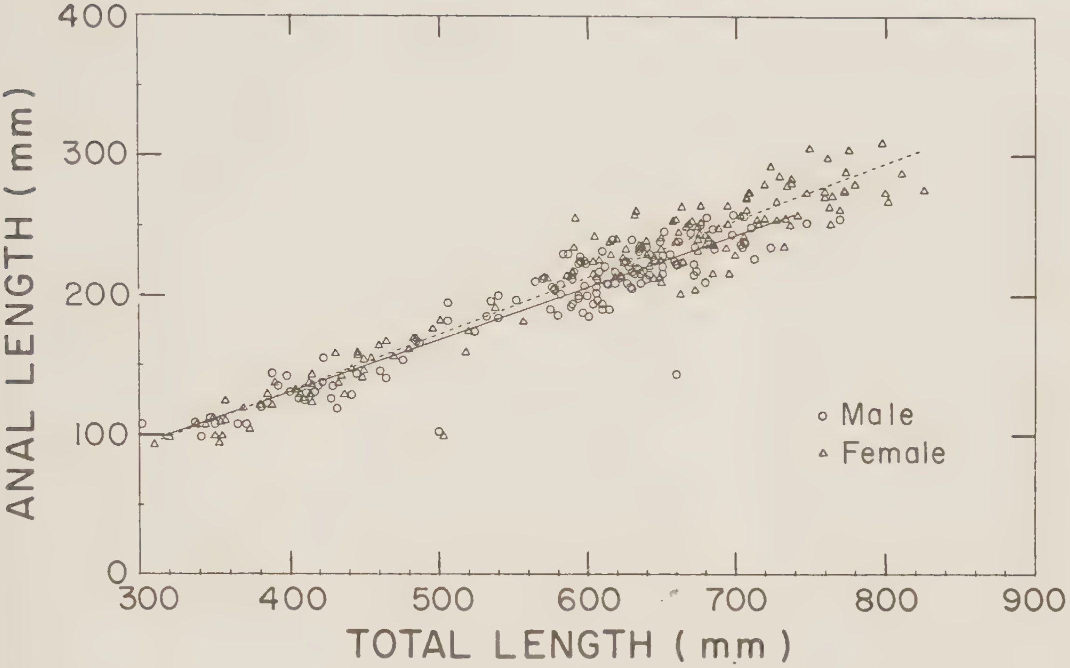

Figure 12.—Relationship of anal length to total length in the Pacific grenadier.

grenadier, *Coryphaenoides rupestris*, roundnose grenadier, made up the bulk of the world catch of the group. From 1975 to 1983 total annual catches from the northeast and northwest Atlantic, mostly by the Soviet Union, ranged from 15,000 to 65,000 t, averaging around 32,000 t (FAO, 1979, 1984). Between 1983 and 1986 however, the catches of roundnose grenadiers have averaged only 17,000 t. On the other hand catches of other species of grenadiers, again mostly by the Soviet Union, have increased rapidly. Between 1983 and 1986 the average catch of grenadiers in the southwest Atlantic (presumably *Macrourus holotrachys* and *M. carinatus*) was 18,000 t, while the catch in the northwest Pacific (presumably *Albatrossia pectoralis*, the giant grenadier) was around 17,750 t[5].

A Soviet report indicated that not only was the flesh of the roundnose grenadier good, but that its liver was also valued because of high oil and vitamin content (Savvatimskii, 1971). Novikov (1970) likewise considered the giant grenadier a valuable food species in spite of its water-logged flesh, because its liver and eggs were rich in vitamins and fats, and because of the apparently large biomass.

In Japan, grenadiers were formerly used to make a minced fish product called "surimi," which was in turn used to produce traditional jellied fish products known as "kamaboko." Pacific grenadier was satisfactory for this purpose as well as for other fish products, but giant grenadier made a poor grade of surimi (Shibata, 1985). With the advent of long-distance trawlers and factory ships, other species, particularly walleye or Alaska pollock, *Theragra chalcogramma*, have taken over this market. Most grenadiers are now caught as a bycatch in trawl fisheries aimed at other species, and the small amount landed is usually used as fish meal or fertilizer. Some species, such as *Coelorinchus tokiensis* are still sought and caught by longline, as they command good prices as food fish[6].

Canadian researchers found that the roundnose as well as another Atlantic species, the roughhead grenadier, *Macrourus berglax*, have good eating qualities and withstand iced or frozen storage better than most fish (Botta and Shaw, 1975, 1976). A similar study of the flesh of Pacific grenadier was reported by Kremsdorf et al. (1979), and their results were almost identical to those of the Canadian researchers, i.e., flesh of Pacific grenadier kept on ice for around 2 weeks did not lose its fresh quality, and taste preference tests showed that it compared favorably with Icelandic cod, *Gadus* sp. Botta and Shaw (1976) also found that 2-day old fish were easier to fillet, and yielded fillets which had better appearance and texture than fresher fish.

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[5] Tomio Iwamoto, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118. Personal commun.

[6] Osamu Okamura, Department of Biology, Kochi University, Kochi 780, Japan. Personal commun.

Sustained catches of roundnose grenadier in the Atlantic have shown that the species can support a substantial fishery. It seems unlikely, based on our fishing experience, however, that Pacific grenadier is abundant enough to warrant a directed fishery off southern and central California. Furthermore the high cost of fishing in deep water, as well as the low flesh yield and presently low price discourages development. But Pacific grenadier can be utilized when caught in deep-sea trawl fisheries directed at other species. The best depths for a mixed species trawl fishery may be around 650 fm where Dover sole, sablefish, and thornyheads are found together with Pacific grenadier (Table 6).

Longline fishing may be a viable alternative to trawls for catching Pacific grenadier because the gear is relatively inexpensive. The method is also effective for catching sablefish, which is more valuable than grenadier. Traditional vertical or horizontal longlines as well as free-vehicle longlines could be used from small vessels. Compared to free vehicle gear, traditional longline gear would require larger winches or line haulers to pull the line. Since long soak times are effective for catching Pacific grenadier, it is possible to space the setting and hauling intervals of free-vehicle longlines to maximize catches.

Further Research

The high number of ripening and spent females caught between late winter and early summer by SIO longlines indicates that this is the period of greatest spawning of Pacific grenadier off southern California. The smallest number of ripe and spent Pacific grenadier was found in late summer to fall, but presence of a few ripening and spent individuals during this period suggests that some spawning occurs throughout the year. Heaviest spawning may occur earlier farther north, as many individuals taken by trawls off Pt. Conception on the *Jordan* in December were either running ripe males or females with spent or enlarged ovaries. In even more northern waters, Savvatimskii (1969) reported ripe females only in October, and Stein and Pearcy (1982) caught ripe females in the fall and in March.

We can only speculate as to our failure to catch ripe females of Pacific grenadier with our longlines. Possibly ripe females stop feeding. It is also possible that they migrate to other areas, or higher up in the water column as has been suggested in the case of roundnose grenadier, because two females and a male of that species in spawning condition were captured about midway between the surface and sea floor over depths of 770-980 fm (1,400-1,800 m) (Grigor'ev and Serebryakov, 1983).

The youngest stages have been found 110 fm (200 m) or less from the surface (Savvatimskii, 1969; Stein, 1980), while larger larvae and juveniles have been caught deeper in the water column. The rarity of the young, considering the high fecundity of the fish, is puzzling. During the SIO-MLRG cruises, only one larva was collected. These poor results are apparently the normal expectations, as demonstrated by Stein's (1980) collection of only 78 larvae and juveniles from 2,700 midwater trawls. Further, despite these sampling efforts, eggs of *C. acrolepis*, which have an outer cover with characteristic hexagonal patterns in ripe females (Boehlert, 1984) are not known to have been collected in the plankton. Neither has a larva with a yolk sac, and there is no evidence that would indicate *C. acrolepis* being viviparous or ovoviviparous. Future studies focused on locating spawning females would certainly be a profitable area of research.

Acknowledgments

We wish to thank Alice Hall for providing data on flesh characteristics of Pacific grenadier. David Woodbury read the otoliths, and Kelly Silberberg helped analyze catch data. William Leet and Sennen Salapare aided us during fishing operations on R/V *David Starr Jordan*. Numerous staff and students from SIO and San Diego State University volunteered their help in the SIO-MLRG cruises. Special thanks to: Ron McConnaughey who took part in all phases of collection of samples at SIO and to Richard Rosenblatt for advice on these cruises and for use of material and data from the SIO Fish Collection. Longline samples were also collected on cruises conducted by Frank Rokop and Joseph F. Siebenaller. Dan Brown of SIO developed several release devices that were used with our free-vehicle longlines. We thank Tomio Iwamoto for reviewing the manuscript and for his helpful comments. The senior author gratefully acknowledges the support of the Marine Life Research Program, the Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigations.

Literature Cited

Alton, M. S. 1972. Characteristics of the demersal fish fauna inhabiting the outer continental shelf and slope off the northern Oregon coast. *In* A. T. Pruter and D. L. Alverson (editors), The Columbia River estuary and adjacent ocean waters; bioenvironmental studies, p. 583-617. Univ. Wash. Press, Seattle.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth. Human Biol. 10:181-213.

Boehlert, G. W. 1984. Scanning electron microcope. *In* H.G. Moser et al. (editors), Ontogeny and systematics of fishes, p. 43-48. Spec. Publ. 1, Am. Soc. Ichthyol. Herpetol.

Botta, J. R., and D. H. Shaw. 1975. Chemical and sensory analysis of roughhead grenadier (*Macrourus berglax*) stored in ice. J. Food Sci. 40:1249-1252.

_________ and _________. 1976. Chemical and sensory analysis of roundnose grenadier (*Coryphaenoides rupestris*) stored in ice. J. Food Sci. 41:1285-1288.

Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12:451-483.

Brothers, E. B., C. P. Mathews, and R. Lasker. 1976. Daily growth increments in otoliths from larval and adult fishes. Fish. Bull. 74(1):1-8.

Brown, D. M. 1975. Four biological samplers: Opening-closing midwater trawl, closing vertical tow net, pressure fish trap, free vehicle drop camera. Deep-Sea Res. 22:565-567.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60: 1-102.

FAO. 1979. Yearbook of fishery statistics, 1978. Food Agric. Organ., U.N., Rome. Vol. 46, 358 p.

_________. 1984. Yearbook of fishery statistics, 1983. Food Agric. Organ., U.N., Rome. Vol. 56, 202 p.

_________. 1988. Yearbok of fishery statistics, 1986. Food Agric. Organ., U.N., Rome. Vol. 62, 479 p.

Gooch, J. A., M. B. Hale, T. Brown, Jr., J. C. Bonet, C. G. Brand, and L. W. Regier. 1987. Proximate and fatty acid composition of 40 southeastern U.S. finfish species. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 54, 23 p.

Gordan, J. D. M. 1979. Lifestyle and phenology in deep sea anacanthine teleosts. *In* P. J. Miller (editor), Fish phenology: anabolic adaptiveness in teleosts, p. 327-359. Symp. Zool. Soc. Lond. 44. Acad. Press, N.Y.

Grey, M. 1956. The distribution of fishes found below a depth of 2,000 meters. Fieldiana, Zool. 36(2):74-336.

Grigor'ev, G. V., and V. P. Serebryakov. 1983. Eggs of rock grenadier, *Coryphaenoides rupestris* (Macrouridae). J. Ichthyol. 23(4):161-163.

Isaacs, J. D., and L. W. Kidd. 1953. Isaacs-Kidd midwater trawl. Scrips Inst. Oceanogr., Oceanogr. Equip. Rep. 1 (SIO Ref. 53-3), 18 p.

________ and G. B. Schick. 1960. Deep-sea free instrument vehicle. Deep-Sea Res. 7:61-67.

Iwamoto, T., and D. L. Stein. 1974. A systematic review of the rattail fishes (Macrouridae:Gadiformes) from Oregon and adjacent waters. Calif. Acad. Sci., Occas. Pap. 111:1-79.

Kremsdorf, D. L., R. V. Josephson, A. A. Spindler, and C. F. Phleger. 1979. Gross composition, sensory evaluation, and cold storage stability of underutilized deep sea Pacific rattail fish, *Coryphaenoides acrolepis*. J. Food Sci. 44: 1044-1048.

Kulikova, E. B. 1957. [Growth and age of deep-water fishes.] Trudy Inst. Okean. Akad. Nauk. 20:347-355 (In Russ., transl. by Am. Inst. Biol. Soc. 1959:284-290).

Leavitt, B. B. 1938. The quantitative vertical distribution of macroplankton in the Atlantic Ocean basin. Biol. Bull. 74:376-394.

Marshall, N. B. 1973. Family Macrouridae. *In* D. Cohen (editor), Fishes of the western North Atlantic, p. 496-662. Mem. Sears Found. Mar. Res. 1, pt. 6.

________ and N. R. Merrett. 1977. The existence of a benthopelagic fauna in the deep-sea. *In* M. V. Angel (editor), A voyage of discovery, p. 483-497. Pergamon Press, N.Y.

Novikov, N. P. 1970. [Biology of *Chalinura pectoralis* in the North Pacific, p. 304-331.] *In* P. A. Moiseev (editor), Soviet fisheries investigations in the north-east Pacific, part 5 (in Russ.). Proc. All-Union Sci. Res.Inst. Mar. Fish. Oceanogr. (VINRO) vol. 70, and Proc. Pac. Sci. Res. Inst. Fish. Oceanogr. (TINRO), vol. 72. (Transl. from Russ. by Isr. Progr. Sci. Transl., Jerusalem, 1972).

Okamura, O. 1970. Studies on the macrouroid fishes of Japan—morphology, ecology and phylogeny. Rep. Usa Mar. Biol. Sta. 17(1-2):1-179.

Pearcy, W. G., and J. W. Ambler. 1974. Food habits of deep-sea macrourid fishes off the Oregon coast. Deep-Sea Res. 21:745-759.

Phleger, C. F. 1971. Biology of macrourid fishes. Am. Zool. 11:419-423.

________ and A. Soutar. 1971. Free vehicles and deep-sea biology. Am. Zool. 11:409-418.

Rass, T. S. 1963. [Deep-sea fishes (Pisces, Macruridae) of the Sea of Okhotsk.], Trudy Instit. Okean. Akad. Nauk 62:211-223. (In Russ., transl. by U.S. Fish Wildl. Serv., Seattle, Wash.)

Saila, S. B., C. W. Recksiek, and M. H. Prager. 1988. Basic fishery science programs. A compendium of microcomputer programs and manual of operation. Develop. Aquacult. Fish. Sci. 18, Elsevier Sci. Publ., N.Y., 230 p.

Savvatimskii, P. I. 1969. [The grenadier of the North Atlantic.] Proc. Polar Res. Inst. Mar. Fish. Oceanogr. (PINRO) 1969:3-72. (In Russ., translated by Fish. Res. Board Can., Transl. Ser. 2879, 1974.)

________ . 1971. Determination of the age of grenadiers (Order Macruriformes). J. Ichthyol. 11(3):397-403.

Shibata, N. 1985. Processing characteristics of underutilized deep-sea cods. Sakana 34:9-28. Tokai Reg. Fish. Res. Lab., Tokyo. (In Jpn.).

Shutts, R. L. 1975. Unmanned deep sea free vehicle system. Scripps Inst. Oceanogr. Mar. Tech. Handb. Ser. TR-61:1-50.

Stein, D. L. 1980. Description and occurrence of macrourid larvae and juveniles in the northeast Pacific Ocean off Oregon, USA. Deep-Sea Res. 27:889-900.

________ and W. G. Pearcy. 1982. Aspects of reproduction, early life history, and biology of macrourid fishes of Oregon, USA. Deep-Sea Res. 29(11A):1313-1329.

Van Dorn, W. G. 1953. The marine release-delay timer. Scripps Inst. Oceanogr., Oceanogr. Equip. Rep. 2 (SIO Ref. 52-23), 10 p.

Wilson, R. R., Jr. 1982. A comparison of ages estimated by the polarized light method with ages estimated by vertebrae in females of *Coryphaenoides acrolepis* (Pisces:Macrouridae). Deep-Sea Res. 29(11A):1373-1379.

________ and R. S. Waples. 1984. Electrophoretic and biometric variability in the abyssal grenadier *Coryphaenoides armatus* of the western North Atlantic, eastern South Pacific and eastern North Pacific Oceans. Mar. Biol. 80: 227-237.

Wimpenny, R. S. 1966. The plankton of the sea. Am. Elsevier, N.Y., 426 p.

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35· Relating Fisheries to the Environment in the Gulf of Guinea: Information, Causality and Long-Term Memory

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Abstract

"Optimal transformations" are new statistical methods that greatly improve our understanding of non-linear relationships that may exist between environmental and ecological data. The effect of "optimal transformations" of environmental data is examined for tuna catches, and for the small pelagic fishery in the Gulf of Guinea. In the frequency domain it is shown that the "optimal transformation" changes the spectrum of the environmental variable so that it is more similar to the spectrum of CPUE (Catch Per Unit of Effort). When there is more than one environmental variable, methods are presented for determining the unique information in each variable that is relevant to the analysis, and for determining if the environmental variables carry information that is not contained in the CPUE series itself. The analysis makes clear why for tuna in some areas wind is most important, while in other areas wind and SST are important. For the small pelagics, the analysis explains why only SST (Sea Surface Temperature) is important for predicting the combined species CPUE, but SST and salinity are both important in predicting the CPUE for *S. maderensis* only. Evidence is presented that the environmental variables important to the fisheries in the Gulf of Guinea have "long-term memory". This has implications for our ability to accurately predict into the future the consequences of our management actions.

Résumé

Les «transformations optimales» sont de nouvelles méthodes statistiques qui améliorent beaucoup notre compréhension des relations non-linéaires qui peuvent exister entre des données environnementales et écologiques. L'effet des «transformations optimales» des données environnementales est examiné pour les captures de thons et de petits pélagiques dans le Golfe de Guinée. Dans le domaine fréquentiel les transformations optimales changent le spectre de la variable environnementale de telle façon qu'il apparaît plus semblable à celui des CPUE (Capture Par Unité d'Effort). Quand plus d'une seule variable environnementale est considérée, des méthodes sont présentées pour déterminer l'information, pertinente pour l'analyse, contenue dans chacune des variables et pour déterminer si les variables environnementales apportent de l'information par rapport aux séries de CPUE. L'analyse révèle pourquoi, pour le thon, le vent est la variable la plus importante dans certaines zones, tandis que pour d'autres il s'agit du vent et de la SST (température de surface de la mer). Pour les petits poissons pélagiques, l'analyse montre pourquoi la SST est importante pour expliquer les CPUE toutes espèces confondues alors que c'est la SST et la salinité qui permettent de prédire la CPUE de *S. maderensis*. On montre enfin que les variables environnementales importantes pour les pêcheries, dans le Golfe de Guinée, possèdent une «mémoire à long terme». Ceci a des implications pour notre faculté à prédire les conséquences des actions d'aménagement.

Introduction

Fisheries management models traditionally have concentrated on the equilibrium behavior of catch and effort in isolation from the environment in which the fish live. In the Gulf of Guinea, as elsewhere, there is mounting evidence that the ocean environment plays a key role in the observed dynamics of fish stocks. A list of references documenting this statement can be found throughout the papers in this volume. I mention in particular Mendelssohn and Roy (1986), and Mendelssohn and Cury (1987, 1989), because the techniques and results of those papers are directly relevant to the concerns of this paper.

Studies of the ocean environment's effects on fish dynamics have occurred at several levels. At the lowest level, studies attempt to determine the direct mechanisms that cause mortality, reproductive success, or growth in a fish. For example, Lasker's work (1978) on the survival of larvae suggests that the concentration of food sources within the first several days of life are essential for survival of the larvae. Such information, if true, provides understanding of the mechanisms by which the ocean affects the fish, and thereby possible limitations of any higher level models. To make practical use of this information, however, would require knowing where the larvae are located and measuring the food concentrations right after birth, a formidable and expensive task.

The next level of study has traditionally looked at contemporaneous environmental conditions in relation to fish catch or fish recruitment. (This approach has been extended, for example, in the papers cited above, by considering the dynamics of both the environment and the fish in space and time). In most of these studies, cross-correlations between variables, such as cross-correlations between sea surface temperature (SST) and catch-per-unit effort (CPUE), have been used to explore the relationships between fish populations and the ocean environment.

It is clear that at this "higher" level, the variables being used no longer directly affect the fish. Rather, they act as surrogates for other variables, or for processes in the ocean, that do directly act on the fish. This is a subtle and a seemingly insignificant distinction, but it is one that will be important for the statistical discussion that follows. For, if the environmental variables being used are not causal, then it makes sense to view the modeling process, particularly in terms of forecasts, as deciding if a variable to be included in the model contains any additional, unique information about the future of the fishery dynamics over and above the information contained in the series itself or in other series to be included in the model.

The cross-correlation between two series at a given lag is not independent of the cross-correlations at other lags nor of the auto-correlations of either series. The most extreme example of this is if each series has an independent deterministic sinusoidal component. Then there is a sinusoid in the cross-correlation function. As a less extreme example, two independent series, each with a large lag-one autocorrelation, over a short period of observation will often have a significant sample cross-correlation at lag-one. This will particularly be true if the underlying series have been time aggregated (Granger 1980).

In the examples above, pre-filtering would have removed some of this spurious correlation. The effect of pre-filtering is to remove some of the information that a series carries about itself. When this removes the cross-correlations, it is tantamount to saying that there is no additional information in the new series. Pre-filtering has its own dangers, but similar characteristics can be searched for in a true multivariate setting. There has been resistance in fisheries to such an approach, because "regressing" CPUE, for example, against lagged values of itself, does not have a clear, causal explanation. If we drop the idea that our models are causal, then it is clear why some such approach makes sense: if lagged values of CPUE can predict future values just about as well as a new variable, then the past history of the CPUE series has integrated into itself any information the new series might have. The past history is not necessary causal, but in terms of information content, it is sufficient.

As I will show, it is possible to resolve some of these issues if we assume that all relationships between CPUE and its own history or between CPUE and the environment is linear. Unfortunately, dating back to some of the earliest Japanese work on fish and the ocean, and to the earlier work on tuna (see Sund et al. 1981 and refences therein for example) the evidence is that the environment affects fish in a nonlinear fashion. The tuna work, based on short term conditions around concentrations of catch, suggests a "window-like" relationship between the environment and tuna CPUE. More recently, using long time-series of data and empirically derived techniques, Mendelssohn and Mendo (1987) have shown the nonlinearities between the environment and recruitment for anchoveta off Peru. Mendelssohn and Cury (1987, 1989) using similar techniques, have shown the nonlinearities in the relationships between CPUE for small pelagics off the Ivory Coast and environmental variables. Cury and Roy (1989) have shown "window-like" relationships between recruitment for eastern boundary current pelagics and transport or turbulence in the particular region.

Such nonlinearites affect the analysis greatly. An environmental variable may not show unique information because it is being examined on the wrong scale. For example, on a linear scale, a window-like relationship will show lack of fit. While I suggest some methods for circumventing this problem, they are ad hoc solutions at best. Using fisheries from the Gulf of Guinea, I will examine ways to determine which variables will be important to include in models, and I will show in specific examples how the analysis changes due to finding a more appropriate scale for the variables.

If the environment is important in fisheries dynamics, then it is to be expected that some of the properties of the ocean's dynamics may be inherited by the fishery dynamics. Recent years has seen a boom in the literature on "chaos" and the related ideas of fractals and fractal dimensions. Probably a more accurate nomenclature is "sensitivity to initial conditions." There is, however, a feature of these concepts that is more relevant to fisheries science. The analyses in this paper assume stationarity (or more exactly joint stationarity) in the series to be studied. Or else it is assumed that the nonstationarity is of a form that can be easily removed, such as a deterministic trend. The physical motivation for these assumptions is that the effect of anything that happens now dies off relatively rapidly. Hurst (1951) noticed that riverflows appeared to have the opposite characteristic - there appeared to be long-term memory in the system. This "Hurst effect", and achieving stationarity by fractional differencing, are closely related to the concepts of chaos and fractals (see for example Mandelbrodt 1983). If the ocean's dynamics exhibit long-term memory, this can have significant implications for how far in the future we can ever expect to accurately forecast fish catches. At the end of this paper I briefly examine the question of long-term memory in the environmental series from the Gulf of Guinea.

Methods

In this section I briefly review some of the relevant literature on "causality" in time-series, and on empirical methods for determining nonlinear transformations of variables in the form of "optimal" additive models. I also discuss in more detail the specific computational techniques used in the next section.

Information between two or more time series

Pierce (1979) developed a time-series analogue to the R^2 statistic of regression analysis for the case of bivariate time series with no feedback. Pierce's statistic measures how much better a second series helps predict a given series over that available from the past history of the series. Parzen (see discussion section of Geweke 1982) pointed out that this amounted to studying the "innovations of the innovation series", a comment which will be made more concrete below. Geweke (1982, 1984) extended these concepts to the true multivariate case with feedback. Other related papers are Gelfand and Yaglom (1959), Caines and Chan (1975), Gustafson, Ljung and Soderstrom (1977) and Anderson and Gevers (1982).

In this paper I follow Gersch (1986), and the presentation closely follows the discussion of that paper. The background for developing a quantitative measure of the information in one time series about another time series (Gelfand and Yaglom 1959) is the measure of the amount of information between two continuously distributed vector random variables X and Y (Shannon 1948, Woodward 1953),

$$I_{x,y} = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} f_{X,Y}(x,y)\ln[f_{X,Y}(x,y)/f_X(x)f_Y(y)]\,dx\,dy \tag{1}$$

where $f_{X,Y}(x,y)$ is the joint probability distribution function of X and Y, and $f_X(x)$, $f_Y(y)$ are the marginal probability distributions of X and Y. Equation (1) is the negative entropy of the "true" distribution $f_{X,Y}$ with respect to the assumed distribution $f_X f_Y$. More formally, equation (1) is the amount of information, on the average, per observation, to reject the null hypothesis that the random vectors X, Y are independent.

In order to use equation (1) simplifying assumptions are necessary. Gelfand and Yaglom (1959) assume that the time series are stationary and jointly normally distributed. Let $w(t)$ be an $(r+q)$ vector-valued time series that consists of an r-vectored time series $x(t)$ and a q-vectored time series $y(t)$, that is $w(t) = (x(t), y(t))^\tau$, and the notation z^τ denotes the transpose of the vector z. Then the spectral density matrix of $w(t)$ at a frequency λ can be partitioned as

$$S_{ww}(\lambda) = \begin{bmatrix} S_{xx}(\lambda) & S_{xy}(\lambda) \\ S_{yx}(\lambda) & S_{yy}(\lambda) \end{bmatrix}$$

Then the Shannon-Gelfand-Yaglom (SGY) measure of information is

$$I_{x,y} \quad = \quad \int_{-\frac{1}{2}}^{\frac{1}{2}} \ln \frac{|S_{ww}(\lambda)|}{|S_{xx}(\lambda)||S_{yy}(\lambda)|}\,d\lambda \tag{2}$$

$$= \int_{-\frac{1}{2}}^{\frac{1}{2}} \ln \frac{|S_{xx}(\lambda)|}{|S_{xx}(\lambda) - S_{xy}(\lambda) S_{yy}^{-1}(\lambda) S_{xy}^{*}(\lambda)|} \, d\lambda \tag{3}$$

$$= - \int_{-\frac{1}{2}}^{\frac{1}{2}} \ln[1 - W_{xy}^{2}(\lambda)] \, d\lambda \tag{4}$$

where S^* denotes the conjugate transpose of the matrix S, and W^2 is the multiple coherence at the frequency λ. In equation (3), if X and Y are independent, then the denominator and numerator are identical and the integral is zero, as would be expected. Equation (4) expresses the information in terms of the extension of the coherence between two series, the multiple coherence.

For arbitrary time series, the SGY measure partitions into

$$I_{x,y} = I_{x \to y} + I_{y \to x} + I_{x \cdot y} \tag{5}$$

where $I_{x \to y}$ is the amount of feedback between the series $x(t)$ and $y(t)$, and $I_{x \cdot y}$ is the amount of instantaneous feedback between the two series (Geweke 1982). The measures in equation (5) can be expressed in terms of linear regressions. Let $|W$ denote conditioning on the present and past of a series, $|W^-$ denote conditioning on the past of a series. Then the series $w(t)$ can be written in equivalent moving average (MA) and autoregressive (AR) forms

$$w(t) = \sum_{i=0}^{\infty} A(i) \epsilon_{t-i}; \qquad Var\{\epsilon_t\} = \Sigma(W|W^-) \tag{6}$$

$$w(t) = \sum_{i=1}^{\infty} B(i) w(t-i) + \epsilon_t. \tag{7}$$

The component series $x(t)$ and $y(t)$ have AR representations

$$x(t) = \sum_{i=1}^{\infty} E_{1i} x(t-1) + u_{1t}; \qquad Var\{u_{1t}\} = \Sigma(X|X^-) \tag{8}$$

$$y(t) = \sum_{i=1}^{\infty} G_{1i} x(t-1) + v_{1t}; \qquad Var\{v_{1t}\} = \Sigma(Y|Y^-) \tag{9}$$

The component series can also be expressed in terms of two different ARMAX models that depend on different present and past information

$$x(t) = \sum_{i=1}^{\infty} E_{2i} x(t-i) + \sum_{i=1}^{\infty} F_{2i} y(t-i) + u_{2t}; \qquad Var\{u_{2t}\} = \Sigma(X|X^-, Y^-) \tag{10}$$

$$y(t) = \sum_{i=1}^{\infty} H_{2i} x(t-i) + \sum_{i=1}^{\infty} G_{2i} y(t-i) + v_{2t}; \qquad Var\{v_{2t}\} = \Sigma(Y|X^-, Y^-) \tag{11}$$

$$x(t) = \sum_{i=1}^{\infty} E_{3i} x(t-i) + \sum_{i=0}^{\infty} F_{3i} y(t-i) + u_{3t}; \qquad Var\{u_{3t}\} = \Sigma(X|X^-, Y) \tag{12}$$

$$y(t) = \sum_{i=0}^{\infty} H_{3i} x(t-i) + \sum_{i=1}^{\infty} G_{3i} y(t-i) + v_{3t}; \qquad Var\{v_{3t}\} = \Sigma(Y|X, Y^-) \tag{13}$$

Then the information measures in equation (5) can be written in terms of the innovations of these ARMAX models (Geweke 1982) as

$$I_{x,y} = \ln \frac{|\Sigma(X|X^-)||\Sigma(Y|Y^-)|}{|\Sigma(W|W^-)|} \tag{14}$$

$$I_{x \to y} = \ln \frac{|\Sigma(Y|Y^-)|}{|\Sigma(Y|X^-, Y^-)|} \tag{15}$$

$$I_{y \to x} = \ln \frac{|\Sigma(X|X^-)|}{|\Sigma(X|X^-, Y^-)|} \tag{16}$$

$$I_{x \cdot y} = \ln \frac{|\Sigma(X|X^-, Y^-)|}{|\Sigma(W|W^-)|} \tag{17}$$

This is the innovations of the innovation series mentioned above.

The amount of information and feedback can be computed in either the time domain or the frequency domain. An important additive decomposition is (Geweke 1982)

$$I_{y\rightarrow x} \geq \int_{-\frac{1}{2}}^{\frac{1}{2}} I_{y\rightarrow x}(\lambda)\, d\lambda \tag{18}$$

with similar relationships for the other measures. (The frequency domain representation is useful for examining environment influences on CPUE, as estimates at different frequencies asymptotically are independent. In the time-domain, it is necessary to adjust for the past history of CPUE. In the frequency domain, only the relationships between CPUE and the environment need be examined).

Model the time series $x(t)$ in two ways - regress it on its own past and on its own past and the past of the series $y(t)$. Let $S_x(\lambda)$ be the power spectrum of $x(t)$ from the regression on its own past, and let $S_{x|x,y}(\lambda)$ be the contribution to the power spectrum of x from its own past when it has been regressed on both x and y. Then

$$I_{y\rightarrow x}(\lambda) = \ln \frac{|S_x(\lambda)|}{|S_{x|x,y}(\lambda)|} \tag{19}$$

If, for example, $y(t)$ does not influence or feedback on $x(t)$ then the inner term in equation (19) is one, and the measure is zero as expected. Geweke (1984) shows that these results continue to hold under conditioning or partial regression on another time series $z(t)$.

To practically implement this, suppose we observe three univariate time series $x(t), y(t)$ and $z(t)$. Assume that there is pairwise linear dependence between the series, that is

$$I_{x,y} \neq 0, \qquad I_{x,z} \neq 0, \qquad I_{y,z} \neq 0. \tag{20}$$

Assume also that each pair of time series is conditioned on the excluded third time series, with the following results,

$$I_{x,y|z} \neq 0, \qquad I_{x,z|y} \neq 0, \qquad I_{y,z|x} = 0. \tag{21}$$

This implies that the the $x(t)$ series uniquely explains the linear relationships between the three series.

Suppose spectral density matrices have been estimated at each frequency and are partitioned as above. Then the coherence between x and y is,

$$W_{xy}^2(\lambda) = \frac{|S_{xy}(\lambda)|}{S_{xx}(\lambda)S_{yy}(\lambda)} \tag{22}$$

The partial spectral densities (conditioned on the excluded variables) are (Brillinger 1981)

$$S_{xx|z}(\lambda) = S_{xx}(\lambda)(1 - W_{xz}^2(\lambda)) \tag{23}$$

$$S_{yy|z}(\lambda) = S_{yy}(\lambda)(1 - W_{yz}^2(\lambda)) \tag{24}$$

$$S_{xy|z}(\lambda) = S_{xy}(\lambda) - \frac{S_{xz}(\lambda)S_{zy}(\lambda)}{S_{zz}(\lambda)} \tag{25}$$

Then the partial coherence between x and y after removing the effects of z is

$$W_{xy|z}^2(\lambda) = \frac{|S_{xy|z}(\lambda)|^2}{S_{xx|z}(\lambda)} \tag{26}$$

Brillinger (1981) gives multivariate extensions for each of these terms. The partial coherences are the frequency domain analogues of partial correlations in regression theory.

The conditions in equations (20, 21) for x to be "causal" can be estimated by

$$W_{xy}^2(\lambda) \neq 0, \quad W_{xz}^2(\lambda) \neq 0, \quad W_{yz}^2(\lambda) \neq 0 \tag{27}$$

$$W_{xy|z}^2(\lambda) \neq 0, \quad W_{xz|y}^2(\lambda) \neq 0, \quad W_{yz|x}^2(\lambda) = 0 \tag{28}$$

Gersch (1986) and Brillinger (1981) give significance tests for each of these quantities. There are a variety of methods for estimating spectral density matrices. In this paper, I have used the autoregressive estimates of Akaike (1980). There is a close connection between AR spectral estimates and Maximum Entropy Spectral Estimation (Ulrych and Bishop 1975).

The AR spectral estimate is calculated by fitting multivariate autoregressive models to the data up to a maximum lag. Akaike's AIC criterion is used to pick the "best" model. Assume this "best" model has m lags, and that the estimated coefficient matrices are given by A_i at lag i. Also let the innovations covariance matrix be denoted by U. Then the spectral density matrix at frequency λ is given by,

$$S(\lambda) = A(\lambda)^{-1} U A^*(\lambda)^{-1} \tag{29}$$

and $A(\lambda) = I - \sum_j^m A_j \exp(-2\iota\lambda j)$ is the Fourier transform of the coefficient matrices.

Estimating nonlinear transformations

The standard linear regression model estimates a function of the form

$$y(i) = a + \sum_j b(j) x_j(i). \tag{30}$$

If it is believed that the relationship between the y's and the x's is nonlinear but of an unknown form, then an acceptable first approximation might be the additive model

$$T(y(i)) = \bar{a} + \sum_j b(\bar{j}) s_j(x_j(i)) \tag{31}$$

where $T(\cdot)$ and the $s_j(\cdot)$ are unknown functions. Breiman and Friedman (1985) have derived an algorithm, the "Alternating Conditional Expectations" algorithm, or ACE, to estimate models of the form of equation (31).

Briefly, for one independent variable, they show this problem is equivalent to finding the transformations that have the highest possible correlation. The quantities that need to be solved for can be written in terms of conditional expectations. The algorithm proceeds by alternately estimating the conditional expectation after removing the influence of the other variables. The conditional expectations are estimated using scatterplot smoothers. The result, therefore, is not a function that can be written down, but rather an empirical transformation of each observed point. The transformation can be observed by plotting the transformed values against the original values. There is a close connection between the ACE algorithm and the power method of calculating the maximum eigenvalue of a matrix (see discussion section of the article).

The ACE algorithm has been used in a fisheries context by Mendelssohn and Cury (1987, 1989), by Mendelssohn and Mendo (1987) , Mendelssohn and Husby (1992), and Cury and Roy (1989). What is noted in each of these papers is that the overall form of the transformations generally have close, obvious physical interpretations. Transformations of CPUE, as would be expected from the ratio of two seperate series, tends to be close to a log scale.

Fractional differencing and long-term memory

My discussion follows Porter-Hudak (1982). Hurst (1951) examined the flows of rivers. Let $x_1, x_2, \ldots, x_T$ be the historical sequence of flows. Then the cumulative flows up to time t are

$$Su_t = \sum_{j=1}^{t} x_j, \qquad t = 1, 2, \ldots, T. \tag{32}$$

Related to reservoir construction is the sequential range

$$R = \max_t Su_t - \min_t Su_t. \tag{33}$$

Hurst looked at the normalized sequential range (or "rescaled adjusted range") where Su_t has the mean flow removed and the quantity is divided by the standard deviation of the flows. If the flows are independent over large time scales then one would expect that $R/S \sim (T/2)^{\frac{1}{2}}$. However, Hurst found that for a wide range of river flows $R/S \sim (T/2)^H$ where H is in the range (.6, .8). Mandelbrot (Mandelbrot and Van Ness 1968, Mandelbrot 1971) explained this in terms of fractional Gaussian noise (fGn). Let $B(s)$ be Brownian motion, a stochastic process such that $B(s+u) - B(s)$ are $N(0,1)$ and independent. Then fractional Brownian motion takes the form

$$B_H(t) = \int_{-\infty}^{t} (t-a)^{H-\frac{1}{2}}\, dB(s) \qquad -\infty < t < \infty \tag{34}$$

or

$$B_H(t) - B_H(0) = \int_{-\infty}^{t} (t-s)^{H-\frac{1}{2}}\, dB(s) - \int_{-\infty}^{0} (-s)^{H-\frac{1}{2}}\, dB(s). \tag{35}$$

Discretizing the equation yields

$$b_t(H) = B_H(t) - B_H(t-1). \tag{36}$$

Fractional Gaussian noise can be described by its autocorrelation function

$$C(s) = (\frac{1}{2})(|s-1|^{2H} - 2|s|^{2H} + |s+1|^{2H}). \tag{37}$$

Fractional Gaussian noise also exhibits the self-similarity property, that is

$$X(t\lambda) \sim (\lambda)^a X(t). \tag{38}$$

A related concept is fractional differencing (Granger and Joyeux 1980, Hosking 1981)

$$(1-B)^d X_t = \epsilon_t \tag{39}$$

where d is possibly nonintegral, B is the backshift operator, and ϵ_t are independently distributed as $N(0, \sigma^2)$. Note that this is not a nonintegral lag operator, but rather an infinitely lagged polynomial in B whose weights die out at a rate given in the autoregressive representation equation (41). The spectral density of this model is

$$f(\lambda) = \frac{\sigma_\epsilon^2}{2\pi}(2(1-cos(\lambda))^{-d} \qquad \lambda \neq 0. \tag{40}$$

Granger and Joyeux (1980) derive the following autoregressive representation of a fractionally differenced process

$$\sum a_j X_{t-j} = \epsilon_t; \qquad a_j = \frac{\Gamma(j-d)}{\Gamma(1-d)\Gamma(j+1)} \qquad j > 1. \tag{41}$$

Porter-Hudak (1982) and Geweke and Porter-Hudak (1983) show that the power spectrums of the error term from an fGn process and a fractionally differenced process only differ by a short-memory component. Thus both models are estimating essentially the same long-term memory component. Porter-Hudak (1982) and Kashyap and Eom (1988) give methods for estimating the fractional differencing parameter d, based on regressions between the log of the periodogram of the observed series and the log of the theoretical spectrum of a fractionally differenced series. The most important property is that long-term memory models have a value of d in the range $(0, \frac{1}{2})$; processes such that $d \geq 1/2$ have infinite variance, and those with $d \leq 0$ are short-term memory models (Granger and Joyeux 1980, Hosking 1981).

Yellowfin Tuna in the Gulf of Guinea

In this section and the next one I make real some of the ideas in the last section, using yellowfin tuna catches in the Gulf of Guinea and catches of small pelagics off the Ivory Coast. Mendelssohn and Roy (1986) studied the space-time dynamics of yellowfin CPUE in the Gulf of Guinea in relation to SST and wind. They divided the northern part of the Gulf of Guinea into 11 areas (fig. 1).

Within each area a local model was estimated that also estimated the missing data (in this instance, whenever there was no fishing in the area there was missing data), using an extension of the EM algorithm (Dempster, Laird and Rubin 1977) suggested by Shumway and Stoffer (1982). Frequency domain principal components and canonical correlations were used to examine phase relationships between the different areas at given frequencies. Mendelssohn and Roy (1986) suggest that yellowfin CPUE follows the propogation of SST in what appears to be a remotely-forced, Kelvin wave type behavior.

The local models suggested that the onset of upwelling previous to fishing was an important key to fishing success. The combined local and global results suggested that SST and wind were surrogate variables for an oceanic process that probably tended to concentrate food for the predatory tunas. There was evidence that the actual relationships were nonlinear, but this was not explored in the paper. The question of which variables in each area were most important in the local models was addressed in at best an ad hoc manner. It is these last two questions that I explore here.

I restrict myself to the coastal areas, areas 7 through 11, where the bulk of the fishing effort has been. It is worth emphasizing that the spectral results given here are average results - at any given time period a variable may be having much more influence on the system than represented in the average statistics.

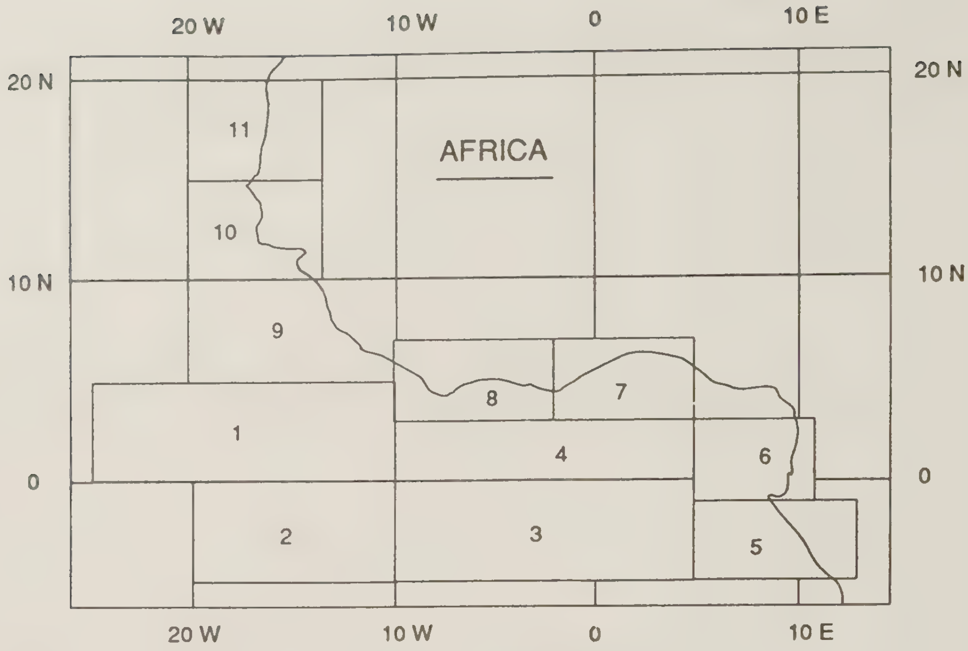

Figure 1: Areas of study for Yellowfin Tuna CPUE.

Area 7

The optimal transformations were estimated arbitrarily up to a lag of two fortnights. The estimated transformation for any variable can be different at each lag, so that ideally each variable at each lag could be treated as a separate variable in the analysis. However, I have arbitrarily used LNCPUE = ln(CPUE + 1.) as the transformation of CPUE, and the estimated transformation at a lag of 1 fortnight for all the environmental variables.

A simple, convenient method for determining the effect of the transformations on a variable is to compare the power spectra of the original and transformed series. This is particularly useful in this situation as it relates nicely to the suggested measures of information in section 2.1 (fig. 2). The LNCPUE series has a smoother spectrum than does CPUE with the peak moved from roughly a period of 7 weeks to a period of 5 weeks.

The estimated transformation for SST (fig. 3) is nearly linear at a lag of one fortnight, but shows a window-like structure with a peak around 27° – 28° C. Despite the near linearity of the transformation at a lag of 1 fortnight, it has a pronounced effect on the spectrum (fig. 4). The peak in the spectrum has been shifted from a period of roughly two months to a period of almost 5 weeks, much closer to the period of LNCPUE.

The estimated tranformation of the north-south wind component is highly nonlinear (not shown), but the effect of the transformation on the spectrum is almost identical to that of SST. The spectrum of the transformed variable is smoother with a peak identical to that of SST. Both the SST series and the north-south wind series have low coherences with CPUE at all frequencies (fig.5-6) while the transformed variables have significant and significantly higher coherences. However, while the coherences and partial coherences for the north-south wind are essentially identical, the partial coherences for SST are greatly lower then the coherences. Carrying out the full analysis in the last section suggests that the significant environmental variable in area 7 is the north-south wind, and that the coherence with SST is due to coherence and feedback between SST and the wind.

Area 8

As in area 7, the spectrum of LNCPUE is shifted over to the higher frequencies with a period of about 5 weeks, but in this case the peak is also much narrower (fig. 7). The estimated transformation for the east-west wind (not shown) is hyperbolic in shape, and its affect on the power spectrum is almost identical to that of CPUE. The estimated

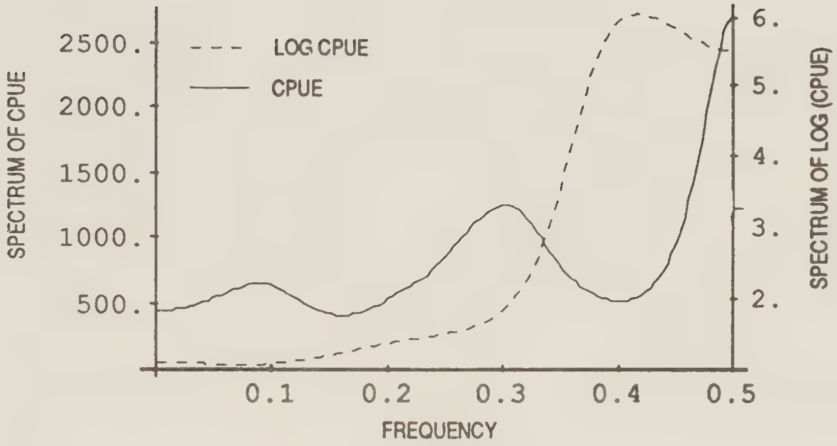

Figure 2: Power Spectrum of CPUE and LNCPUE in area 7.

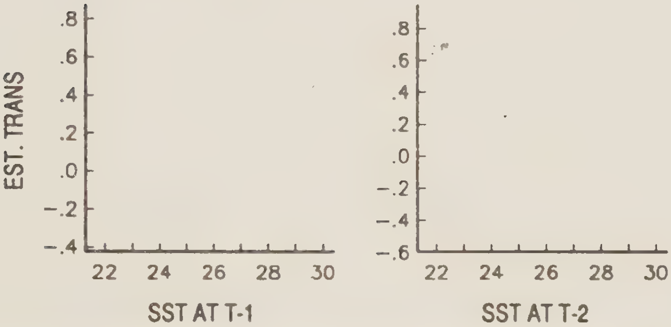

Figure 3: Estimated transformation of SST in area 7 from the ACE algorithm at lags of one and two fortnights.

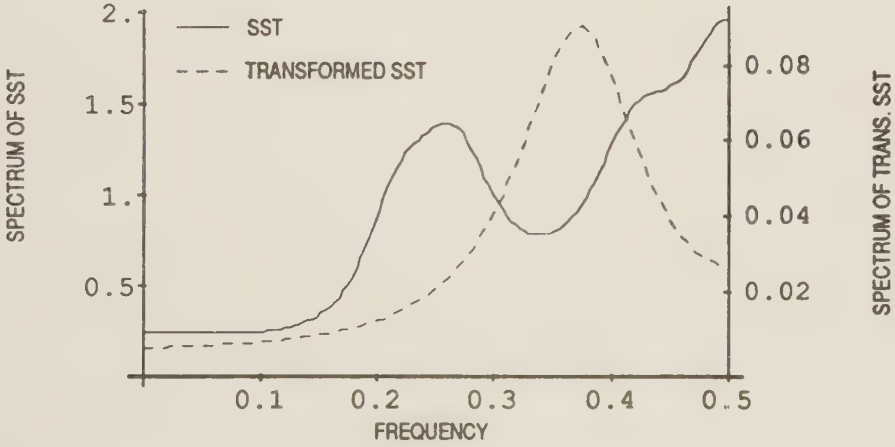

Figure 4: Estimated power spectrum of raw and transformed SST in area 7.

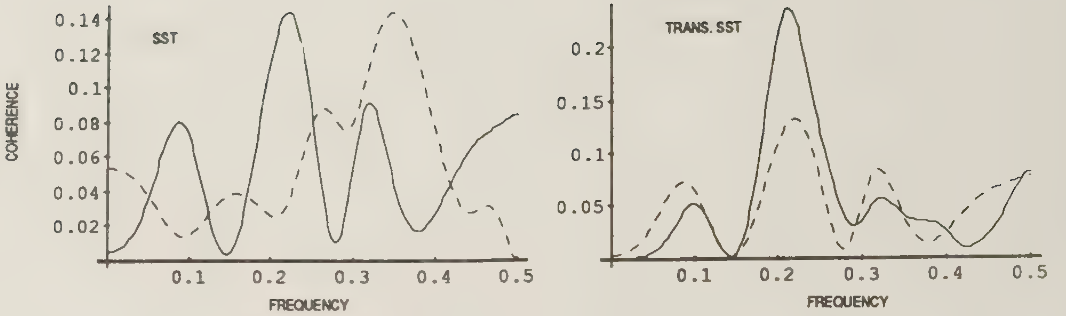

Figure 5: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with SST and LNCPUE with transformed SST in area 7.

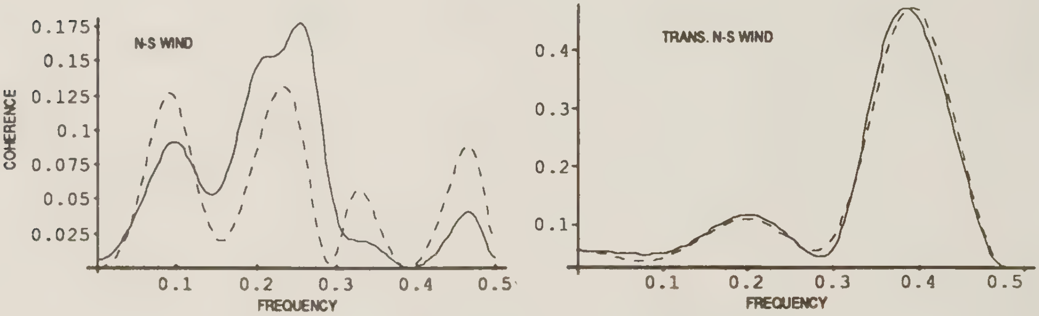

Figure 6: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with north-south wind and LNCPUE with tranformed north-south wind in area 7.

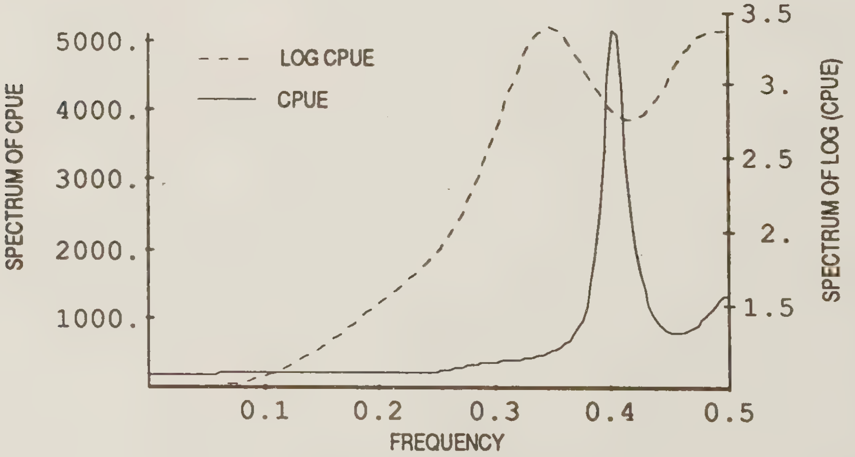

Figure 7: Power spectrum of CPUE and LNCPUE in area 8.

transformation of the north-south wind is again highly non-linear (not shown), and the power spectrum is transformed much as with CPUE and the east-west wind.

The transformation of SST at a lag of 1 fortnight is almost window-shaped (fig. 8) The transformation smooths the power spectrum shifting the power into the highest frequencies at a period of around 1 month. While the coherences of both raw and untransformed east-west wind are high, the partial coherences of both at all frequencies are non-significant. (This is true for areas 9 through 11 also, so this variable will not be examined further). The coherence between CPUE and SST, particularly with the raw series, is particularly significant at a period of roughly 5 weeks (fig. 9). The partial coherences between CPUE and SST are essentially insignificant. The partial coherences between LNCPUE and SST are insignificant except at a period of 1 month.

The coherences and partial coherences between CPUE and north-south wind are almost identical (fig.10), while with the transformed data, one peak at a period of 1.5 months is sharply reduced. However, the overall results are the same as with area 7 - north-south wind is the predominant environmental variable, working at relatively high frequencies, and with an additional effect due to SST on the transformed scale at a period of one month. The transformed data has in effect separated out the frequencies at which the wind and SST contain important information about CPUE. However, at most frequencies, the observed coherence between SST and CPUE appears to be due to feedback and coherence between SST and the wind.

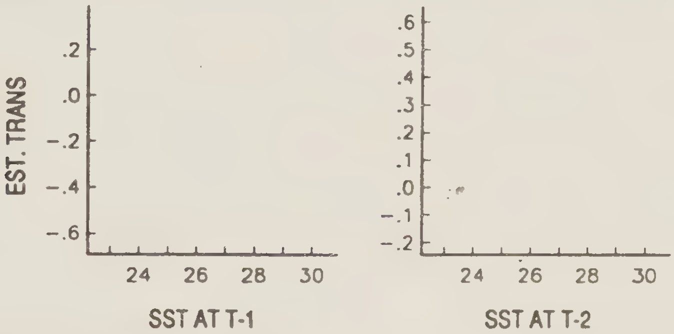

Figure 8: Estimated optimal transformation of SST at a lag of one and two fortnights in area 8.

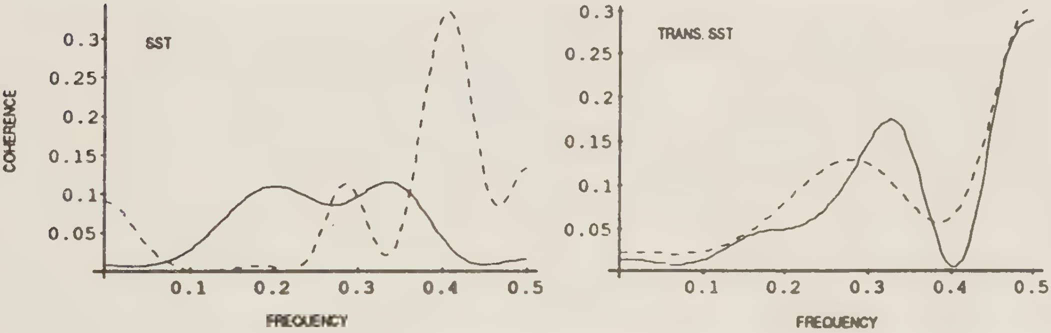

Figure 9: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with SST and LNCPUE with transformed SST in area 8.

Area 9

The spectra for CPUE and LNCPUE in this area are nearly identical with a sharp peak at a period of slightly greater than one month (not shown). The transformation of the north-south wind (fig. 11) is window-shaped, and transforms the power spectrum to a single peak at the same frequency as that of CPUE (fig. 12).

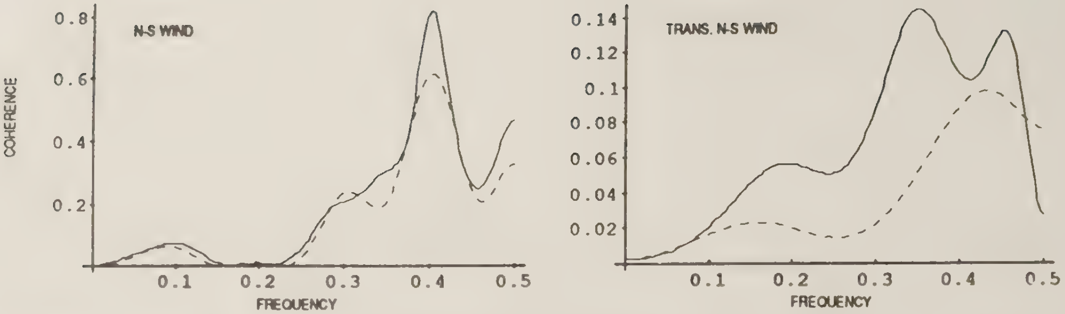

Figure 10: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with north-south wind and LNCPUE with transformed north-south in area 8.

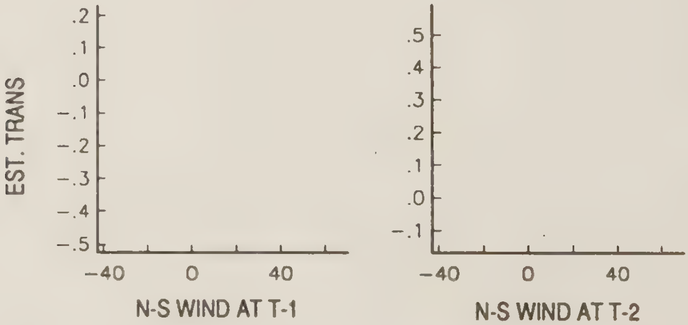

Figure 11: Estimated transformation for north-south wind in area 9.

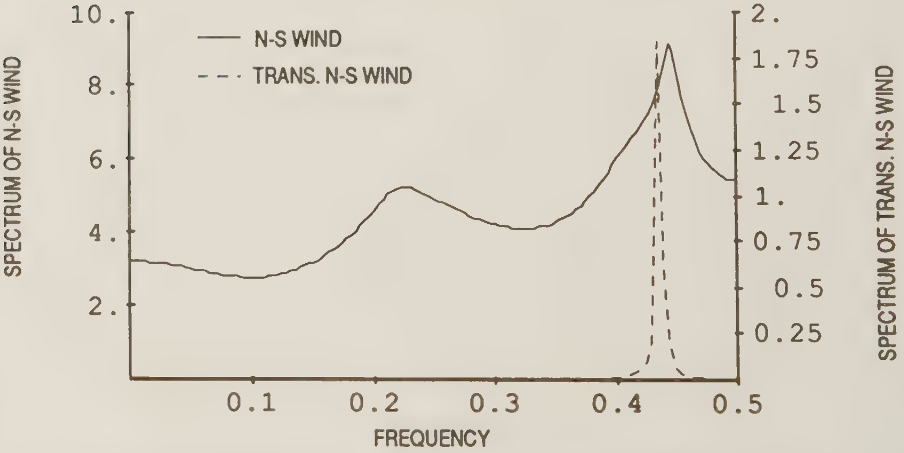

Figure 12: Estimated spectra of raw and transformed north-south wind in area 9.

The coherences and partial coherences between CPUE and north-south wind are similar (fig. 13), but with the transformed data a very significant peak in the coherence disappears in the partial coherence. A similar result can be seen for SST (fig. 14). Here the high-frequency peak in the coherence disappears, while a lower frequency peak remains. This is evidence that at the peak frequency, SST and the north-south wind contain nearly identical information about the environment.

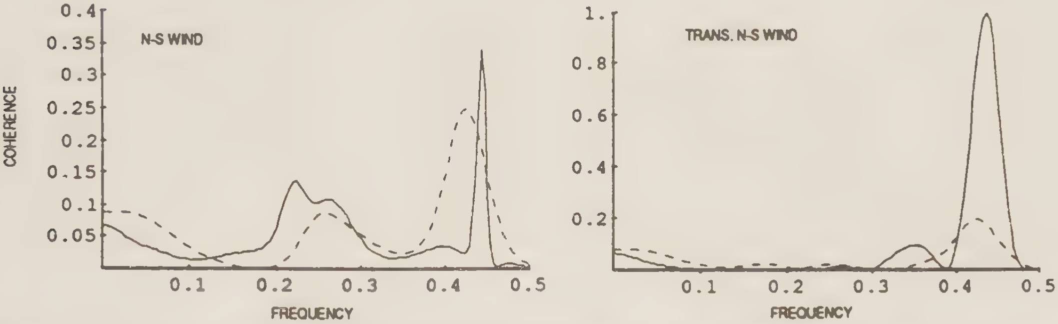

Figure 13: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with north-south wind and LNCPUE with transformed north-south wind in area 9.

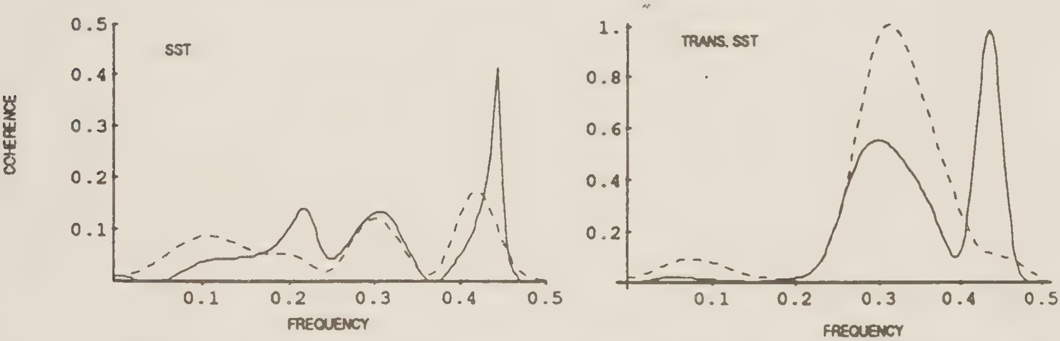

Figure 14: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with SST and LNCPUE with tranformed SST in area 9.

Areas 10 and 11

In area 10, the estimated transformations for both the north-south wind and SST are nearly linear (not shown). For both variables, however, the effect on the estimated power spectrum is to shift a single peaked spectrum from a frequency of .45 to a frequency of .4 (not shown). For the raw data, the peaks in the coherences with either environmental variable disappear in the partial coherences (fig. 15 and 16). As these peaks occur at the same frequencies for both SST and the north-south wind, this implies that both variables contain similar information about the ocean in terms of CPUE for yellowfin. On the transformed scale, the coherences and partial coherences for LNCPUE with transformed SST are nearly identical, while those with the north-south wind are reduced at the peak frequency. However, at this peak frequency the partial coherence with the north-south wind is still significant, so that both wind and SST contain unique information when the data are appropriately transformed.

The situation is very similar in area 11, where SST and north-south wind both are significant at a period of roughly 2 months. Each variable contains some overlapping information at this frequency, but the partial coherences are also significant though smaller than the coherences.

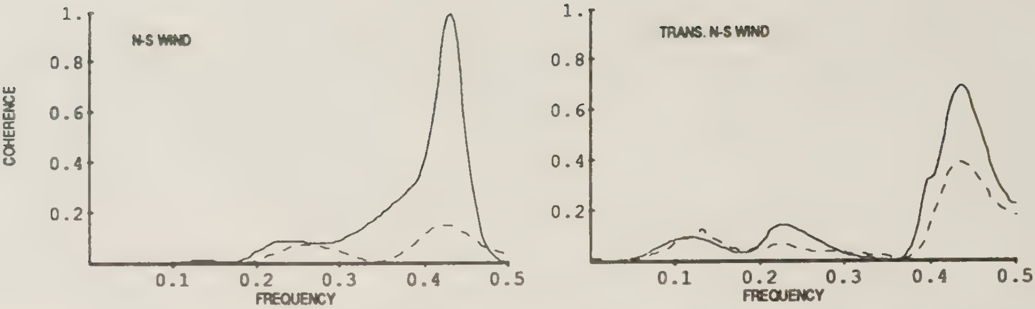

Figure 15: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with north-south wind and LNCPUE with transformed north-south wind in area 10.

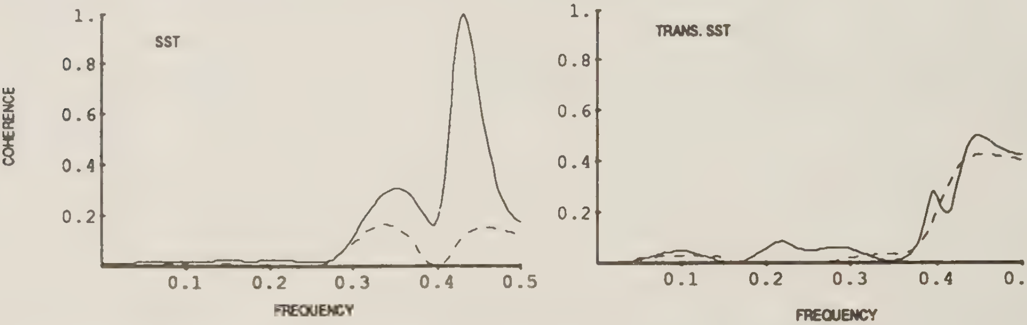

Figure 16: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with SST and LNCPUE with transformed SST in area 10.

Small pelagics off the Ivory Coast

Mendelssohn and Cury (1988) estimate forecasting models and nonlinear transformations for the explanatory variables for modeling the CPUE of small pelagics off the Ivory Coast. Mendelsson and Cury (1989) also study the dominant species in the catch, *Sardinella maderensis*, in time, as well as in space and time. Their results suggests that the factors affecting the aggregate CPUE are not the same as those affecting *S. maderensis* by itself. In this section I reexamine this question using the techniques of this paper.

I have arbitrarily estimated the optimal transformations for the explanatory variables from a model which includes lags up to 4 fortnights. Thus, each model contains lagged values of CPUE, lagged values of SST at 5 meters depth from a shore station (SST5M) and salinity at 5 meters depth (SAL5M) from the same station.

Log of CPUE again is used as the transformation for CPUE. LNCPUE shifts the spectrum from a peak at around a period of 1 month to a peak centered around 5 weeks (fig. 17). The estimated transformations for SST5M and SAL5M (fig. 18,19) shift their power spectra in a similar manner so that all three series have a peak in their spectrum at a period of roughly 5 weeks (fig. 20,21).

The coherences and partial coherences for SST5M with CPUE are nearly identical (fig. 22). The coherences make clear how the transformation has shifted the spectrum so that it is closely aligned with LNCPUE.

The coherences for CPUE with SAL5M show a strong coherence at a period of 1 month, but this disappears in the partial coherence (fig. 23). On the transformed scale, while the coherences and partial coherences are similar, they are not particularly significant. This supports the claim in Mendelssohn and Cury (1987) that for combined CPUE, SST5M was sufficient for prediction and that no extra information was contained in the SAL5M series.

When examining CPUE for *S. maderensis* only, the picture is different. The coherences and partial coherences for SST5M with CPUE are nearly identical, with a significant peak at a period of roughly 2 months (fig. 24,25). For SAL5M, the coherences and partial coherences are identical expect at this frequency, where a significant peak in the coherence is eliminated. The most significant coherence for CPUE with SAL5M is now at a period of roughly a month.

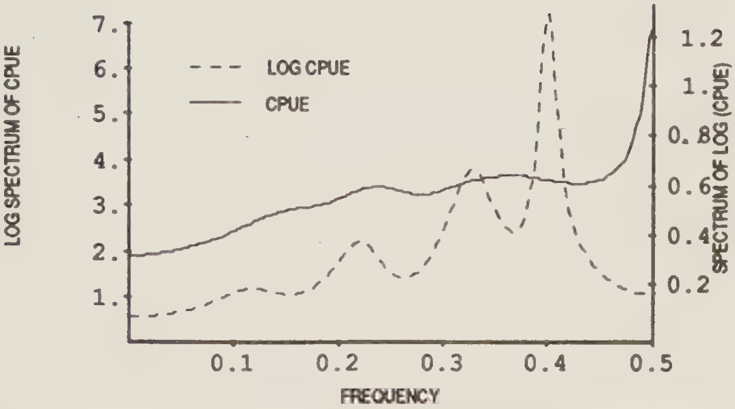

Figure 17: Estimated power spectrum for CPUE and LNCPUE for small pelagics off the Ivory Coast.

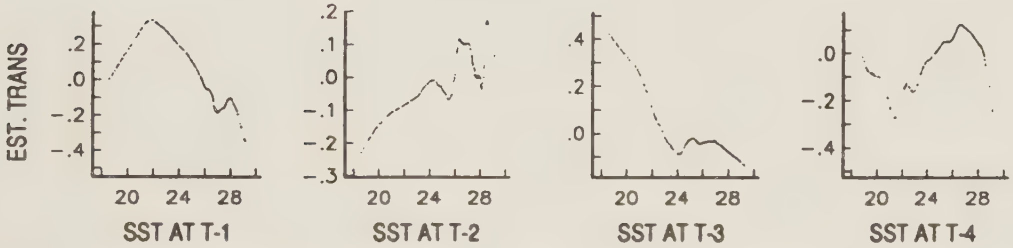

Figure 18: Estimated transformations for SST5M off the Ivory Coast.

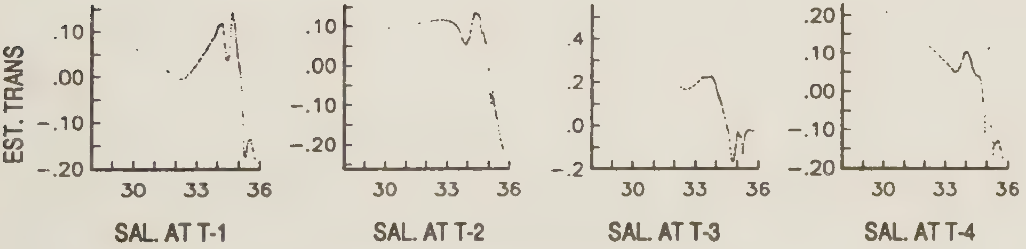

Figure 19: Estimated transformations for SAL5M off the Ivory Coast.

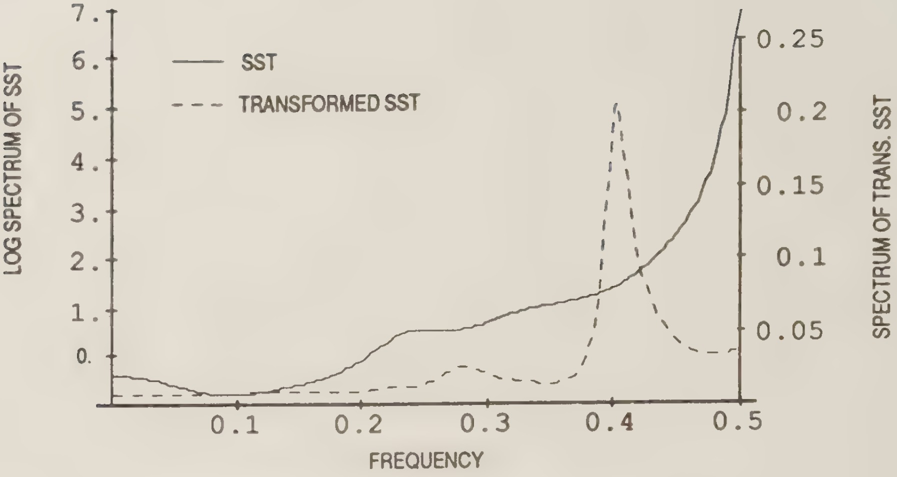

Figure 20: Estimated power spectrum for SAL5M off the Ivory Coast.

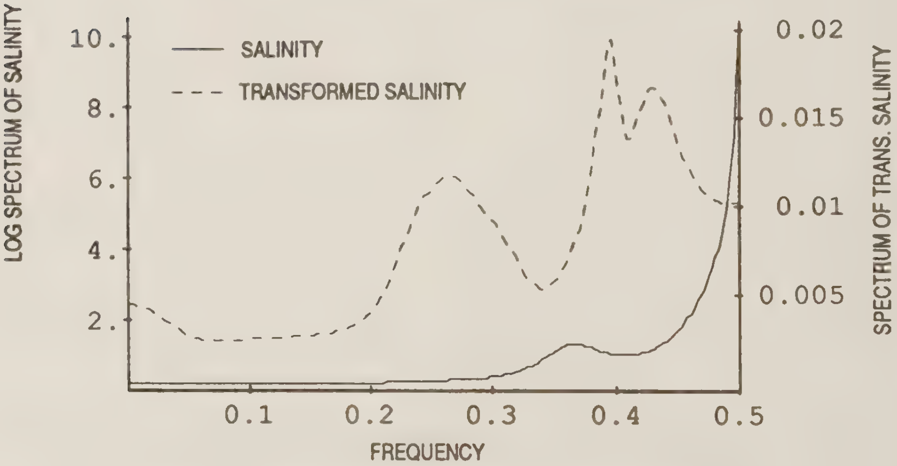

Figure 21: Estimated power spectrum for SAL5M off the Ivory Coast.

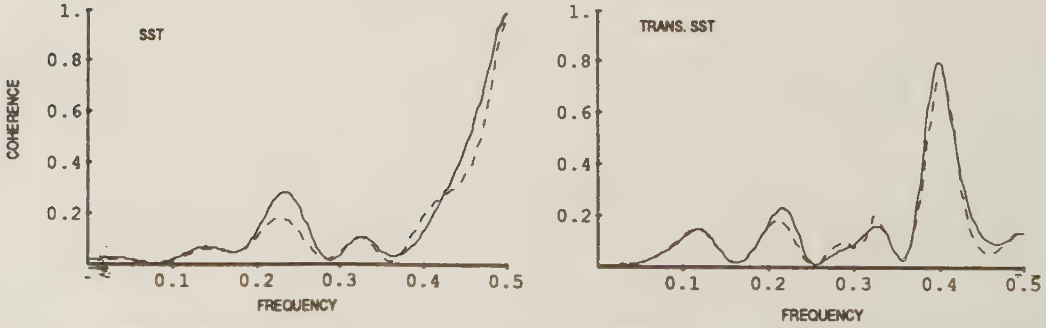

Figure 22: Coherences (solid lines) and partial coherences (dashed lines) for CPUE with SST5M and LNCPUE with transformed SST5M for small pelagics.

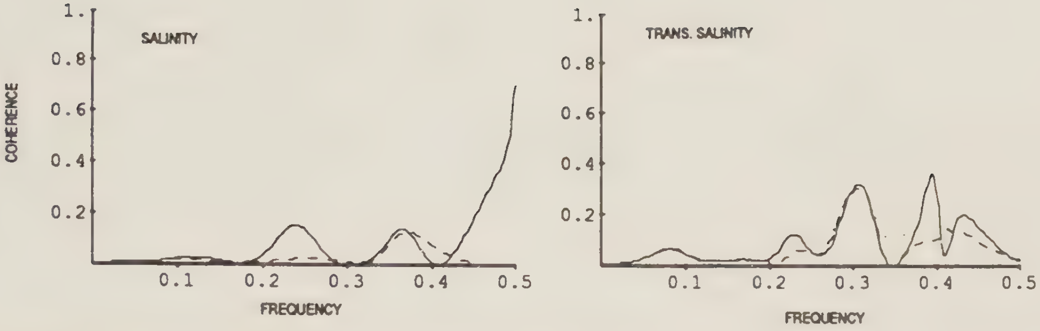

Figure 23: Coherences (solid lines) and partial coherences (dashed line) for CPUE with SAL5M and LNCPUE with transformed SAL5M for samll pelagics.

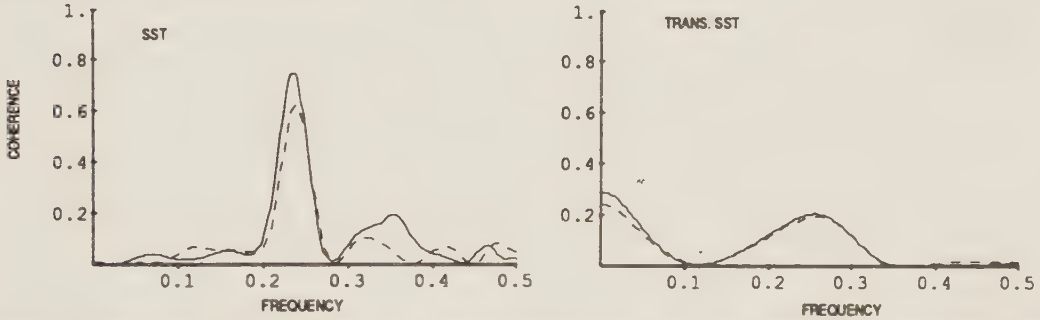

Figure 24: Coherences (solid lines) and partial coherences (dashed line) for CPUE with SST5M and LNCPUE with transformed SST5M for *S. maderensis*.

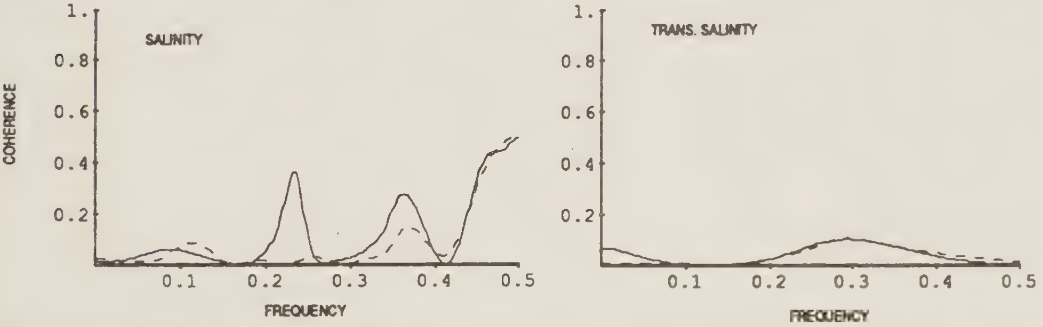

Figure 25: Coherences (solid lines) and partial coherences (dashed lines) between raw and transformed SAL5M and raw and transformed CPUE for *S. maderensis*.

Thus, for *S. maderenis*, the partial coherences show SST5M and SAL5M both containing significant information about CPUE, but at different frequencies. That SAL5M is important for *S. maderensis* but not for combined CPUE was asserted by Mendelssohn and Cury (1989) using time-domain techniques. Here I show further evidence of the claim.

The low coherences in the transformed data for *S. maderensis* is due to the fact that I have arbitrarily used the transformation at a lag of 1 fortnight. Particularly for SAL5M, it is clear from the analysis of Mendelssohn and Cury (1989) that salinity has its greatest effects at much longer lags. There are significant and difficult management questions raised by the fact that the dynamics of the combined CPUE (that faced by the fishermen) are much different from that of the dominant species in the catch. Clearly, a forecast of the aggregate could become misleading, and it may be preferable to aggregate forecasts instead.

Long-term memory in the ocean environment in the Gulf of Guinea

In this section I briefly consider if there is long-term memory in the ocean environment in the Gulf of Guinea. The presence of long-term memory may have profound implications for fisheries management. If long-term memory exists in the ocean, then small changes in the ocean, rather than dying out and causing bounded changes, persist and their effects may multiply through time. Large changes, such as El Nino type events, can have lasting consequences. If the ocean exerts a significant influence on the dynamics of a fish population, then it can be expected that fish populations will display a similar property. This would limit how far into the future we can reasonable expect to understand the consequences of management regimes on the fishery.

I examine the question of the presence of long-term memory by calculating estimates for the fractional differencing parameter d in equations (38) and (39) for several of the environmental series. I use the shore station SST and salinity series (SST5M and SAL5M) as probably reflecting the environmental conditions relevant to the important near-shore fisheries. I also use SST and the two wind component series from area 9, which is the area of the Intertropical Convergence Zone. This area most likely will reflect much of the dynamics of the Gulf. The salient feature here is that short-term memory series have a value between $(-1/2, 0)$, long-term memory models have a value of d between $(0, 1/2)$, and series with a value of d greater than $1/2$ have infinite variance.

The estimates of d (table 1) suggest that all of the series except the east-west component of the wind have a strong long-term memory component.

	Method of Estimation	
Series	Geweke & Porter-Hudak	Kashyap & Eom
SST5M	0.4170	0.4426
SAL5M	0.4241	0.4486
Area 9 SST	0.6169	0.6728
Area 9 NS Wind	0.4036	0.4312
Area 9 EW Wind	0.0021	-0.0070

Table 1: Estimates of the fractional differencing parameter for selected environmental series in the Gulf of Guinea.

There is some evidence that SST may even be an infinite variance series. If this is so, climatologies and other mean-like statistics in this region would have very little meaning. SST in the Gulf of Guinea appears to reflect important processes in the Gulf of Guinea that have major influences on fish dynamics, and my results suggest that these processes may have infinite variance. While much more research must be done in this area before any definitive statements can be made, the initial evidence is troubling indeed.

References

Akaike, H. 1980. On the identification of state space models and their use in control. *In*: D. Brillinger and G. Tiao (eds.), Directions In Time Series. Proceedings of the IMS Special Topics Meeting on Time Series Analysis, Ames, Iowa 1978. Institute of Mathematical Statistics, Hayward.

Anderson, B.D.O. and M.R. Gevers. 1982. Identifiability of linear stochastic systems operating under linear feedback. Automatica, 18:195-213.

Brillinger, David R. 1981. Time Series: Data Analysis and Theory, (Expanded Edition). San Francisco, Holden-Day.

Breiman, L., and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. J. Am. Stat. Assoc., 80: 580-619.

Caines, P.E. and C.W. Chan. 1975. Feddback between stationary stochastic processes. IEEE Transactions on Automatic Control AC-20:498-508.

Cury, P. and C. Roy. 1989. Optimal environmental windows and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci., Vol. 46 (4): 670-680.

Dempster, A.P., N.M. Laird and D.B. Rubin. (1977). Maximum likelihood from incomplete data via the EM algorithm. J. Roy. Statist. Soc., Ser. B. 39:1-38.

Gelfand, I.M. and A.M. Yaglom. 1959. Calculation of the amount of information about a random function contained in another such function. American Mathematical Society Translations, 12: 199-246.

Gersch, Will. 1986. Modeling multivariate covariance nonstationary time series and their dependent structure. Unpublished manuscript, Dept. of Information and Computer Sciences, University of Hawaii.

Geweke, John. 1982. The measurement of linear dependence and feedback between multiple time series. (With discussion). J. Am. Stat. Assoc., 77:304-351.

Geweke, John. 1984. Measures of conditional linear dependence and feedback between time series. J. Am. Stat. Assoc., 79:907-915.

Geweke, J. and S. Porter-Hudak. 1983. The estimation and application of Long Memory Time Series Models. J. Time Series Anal., 4:221-238.

Granger, C.W.G. 1980. Long memory relationships and the aggregation of dynamic models. J. Econometrics, 14:227-238.

Granger, C.W.G. and R. Joyeux. 1980. An introduction to long memory time series models and fractional differencing. J. Time Series Anal., 1:15-29.

Gustafson, I., L. Ljung, and T. Soderström. 1977. Identification of processes in closed loops - Identifiability and accuracy aspects. Automatica, 13:59-75.

Hosking, J.R.M. 1981. Fractional differencing. Biometrika, 68:165-176.

Hurst, H.E. 1951. Long term storage capacity of reservoirs. Trans. Amer. Soc. Civil. Engrs., 116:770-799.

Kashyap, R.L. and Kie-Bum Eom. 1988. Estimation in long-memory time series models. J. Time Series Anal., 9:35-42.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Reun. Cons. Int. Explor. Mer, 173:212-230.

Mandelbrot, B.B. 1971. A fast fractional Gaussian noise generator. Water Resources Research, 7:543-553.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature. W.H. Freeman and Company, New York, 468p.

Mandelbrot, B.B. and J.W. Van Ness. 1968. Fractional Brownian motion, fractional noises and applications. SIAM Review, 10:422-437.

Mendelssohn, R. and P. Cury. 1987. Forecasting a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. Can. J. Fish. Aquat. Sci., 44:408-421.

Mendelssohn, R. and P. Cury. 1989. Temporal and Spatial Dynamics of a Coastal Pelagic Species, *Sardinella Maderensis* Off the Ivory Coast. Can. J. Fish. Aquat. Sci., 46(10):1686-1697.

Mendelssohn, R. and D. Husby. 1992. Space-Time Analysis and Forecasting of Albacore Catch-per-unit-effort in Relation to the Ocean Environment. Manuscript in preparation.

Mendelssohn, R. and C. Roy. 1986. Environmental influences on the French, Ivory Coast, Senegalese and Moroccan tuna catches in the gulf of Guinea. p.170-188, *in*: Special Publication of the International Skipjack Year Program, ICCAT, Madrid.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series. *In*: D. Pauly and I. Tsukayama (eds.), The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change. ICLARM, Manila, p.294-306.

Pierce, David A. 1979. R^2 measures for time series. J. Am. Stat. Assoc., 74:901-910.

Porter-Hudak, Susan L. 1982. Long-Term Memory Modelling - A Simplified Spectral Approach. Ph.D. Thesis, Department of Statistics, University of Wisconsin, Madison.

Shannon, C.E. 1948. A mathematical theory of communication. Bell Systems Technical Journal, 27:379-423, 623-656.

Shumway, R.H. and D.S. Stoffer. 1982. An approach to time series smoothing forecasting using the EM algorithm. J. Time Series Anal., 3:253-264.

Sund, P.N., M. Blackburn and F. Williams. 1981. Tunas and their environment in the Pacific ocean: A review. Oceanogr. Mar. Biol. Ann. Rev., 19:443-512.

Ulrych, T.J. and T.N. Bishop. 1975. Maximum entropy spectral analysis and autoregressive decomposition. Rev. Geophys. Space Phys., 13:183-200.

Woodward. P.M. 1953. Probability and Information Theory with Applications to Radar. McGraw-Hill, New York.

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Age and growth of *Lutjanus kasmira* (Forskål) in Hawaiian waters

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The growth of Hawaiian taape, *Lutjanus kasmira*, was studied by examining otoliths and by analysing length–frequency distribution. Annual hyaline and opaque markings were visible in whole mounts of sagittae, which were verified by enumeration of daily increments with a scanning electron microscope (SEM) and through marginal increment analysis. The von Bertalanffy growth curve was fitted to the data, resulting in:

$$\text{T.L.} = 34{\cdot}0\,\{1\text{-exp}[-0{\cdot}29(t+1{\cdot}37)]\}$$

where T.L. is total length (cm) and t is age (years). SEM observations revealed that the slow-growth hyaline zones were composed of daily increments too small (0·4–0·8 μm) to be resolved optically. Thus, age estimates derived by numerically integrating otolith growth rate data obtained with a light microscope showed a negative bias, resulting in overestimation of growth rates. Parameter estimates obtained from three different types of length–frequency analysis were also unstable. This was due, at least in part, to differences in the size composition of fish sampled with different fishing gears and from different depths.

The growth rate registered in Hawaii falls within the reported growth coefficients of lutjanids, whereas it is one of the highest in the Pacific and clearly higher than a deep-water lutjanid species growth in Hawaii. Probably, this high growth rate may have been enhanced by the relative lack of competitors in the depauperate Hawaiian marine fish community.

Key words: growth; otolith; daily growth rings; Lutjanidae; Hawaii.

I. INTRODUCTION

With its great isolation from other island ecosystems, the Hawaiian Archipelago is known for its relatively depauperate nearshore marine fish fauna. One of the most striking features of this community is the complete absence of native shallow-water snappers (Lutjanidae) and groupers (Epinephelinae), two ubiquitous taxa occurring on shallow reefs elsewhere in the tropical Indo-Pacific. As a consequence, a number of attempts have been made to introduce these commercially valuable fishes to Hawaii. The most successful of these has been taape, *Lutjanus kasmira* (Forskål), which was first released from the island of Oahu late in the 1950s (Randall, 1960); within 10 years it had spread to all other major islands of the archipelago.

Taape were first legally fished in 1966, and landings have increased rapidly, with a reported commercial catch of 36 700 kg in 1981. The present population is quite large and, based upon a trophic analysis of gut contents (Oda & Parrish, 1981), the introduction of taape is thought to have adversely affected populations of native

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species. Beyond this single study, however, the population dynamics and community ecology of taape in Hawaii have not been studied, despite its remarkable population growth and increased importance to local fisheries.

The study of tropical fish growth has been a persistent problem due to poorly developed growth marks in the hard parts of most species and what, characteristically, are extended periods of spawning activity (Brothers, 1980). A broad reproductive period tends to obscure the distinction among cohorts in length–frequency data. Therefore, we studied taape growth using several independent approaches, including both otolith and length–frequency analysis. The general problem of determining age in tropical species is also discussed in the light of our more specific findings relating to the growth of taape in Hawaiian waters.

II. MATERIALS AND METHODS

In 1987, taape were sampled at several fish markets on Oahu and during a cruise of the RV 'Townsend Cromwell'. In the laboratory the total length (T.L., cm) and sex of each fish was determined. The monthly percentage of sexually mature females (i.e. vitellogenesis to post-spawning inclusive) was determined to assess the timing of the spawning season.

OTOLITH STUDIES

Sagittae were extracted from all specimens, cleaned, and stored dry in vials. Although some of the otoliths ($N=15$) were examined with a scanning electron microscope (SEM), most were studied with light microscopes, both dissecting and compound. When observed with a dissecting microscope under reflected light in a black Petri dish while immersed in a dense clarifying medium such as glycerine, taape otoliths show a concentric pattern of opaque and translucent rings. These rings are generally believed to be deposited during periods of fast and slow growth, respectively (Williams & Bedford, 1974). We studied the periodicity and timing of ring formation through marginal increment analysis, i.e. the percentage of otoliths having opaque margins was plotted for each month sampled. Once the annual periodicity of the rings was confirmed, an age–length relationship was estimated by fitting the von Bertalanffy growth equation to the data using Marquardt's algorithm.

For SEM study the otoliths were sagittally sectioned and preparations were glued to SEM statives with colloidal silver and polished with 0·3-μm alumina. The otolith surface was then cleaned and etched 40 s with 1% HCl, washed, and dried overnight in an oven at 80° C to reduce electric changes during observation. Finally, samples were sputter-coated with gold-palladium and viewed with a Hitachi S-570 SEM at the Instituto de Ciencias del Mar using 15 kV tension. Using magnification, the rings were seen to be composed of differentiated daily growth increments (Pannella, 1971). The number of increments in a growth cycle (i.e. one opaque ring and its adjacent translucent ring) was compared with the number of days in a year, to evaluate the periodicity of ring formation.

An additional otolith subsample ($N=31$) was prepared for study with compound light microscopy. These were embedded in casting resin and 0·7-μm sections were cut through the frontal plane (focus to most distal portion of postrostrum). Samples were polished and mounted on glass slides with Euparol for observation. The otoliths were viewed using a semi-automatic image analysis system (Biosonics Optical Pattern Recognition System*). Daily increment widths were measured to estimate the growth rate of the otolith at specific sites along the focus-postrostrum growth axis. The exact location of each site was determined by measuring the distance to the otolith focus. Numerical integration of the data provided estimated of age (years) at fixed 500-μm increments in length to the otolith. Otolith length was then used to predict T.L. with an equation obtained by regressing the natural logarithm of T.L. on the logarithm of the radial length of the otolith. The weighted T.L. and age data were then fitted to the von Bertalanffy growth equation using non-linear regression. Ralston & Williams (1989) provide a detailed description and evaluation of this method, which depends upon a close coupling between somatic and otolith growth.

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*Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The Hotelling's T^2 multivariate statistical procedure (Bernard, 1981) was used to test the differences in growth between the Hawaiian taape and taape in other areas where it is indigenous.

LENGTH–FREQUENCY ANALYSIS

Three sets of data were used in the length–frequency analysis. Two were collected off Oahu in July 1978 and April 1979 (samples 1978 and 1979) by scuba divers setting a bottom gill net near a school of taape at 15 m depth and herding the fish into the net (J. D. Parrish, Hawaii Cooperative Fishery Research Unit, Honolulu). The third was collected by hook-and-line fishing in 40 m of water during a research cruise in September 1987 off the island of Niihau (sample 1987).

The regression method of Wetherall *et al.* (1987) was used to obtain a first estimate of L_∞. The von Bertalanffy growth curve was then fitted to the three length–frequency data sets using the ELEFAN I procedure (Pauly & Gaschutz, 1979).

An additional combined analysis of otolith and length–frequency data was performed, wherein mean T.L. at annulus statistics obtained from examination of translucent and opaque marks in the otoliths were restructured to resemble tag–recapture data. Annual growth increments were calculated from successive lengths at age as if they were recaptures 1 year later. Deterministic selection of the growth increments by the ELEFAN V computer program (Brey & Pauly, 1986) was used to jointly analyse the length–frequency and otolith data, following the approach used by Morgan (1987).

III. RESULTS

OTOLITH STUDIES

Taape otoliths, when observed with a dissecting microscope, showed a concentric pattern of broad translucent (i.e. hyaline) and diffuse opaque rings. Slight movements of the light source helped in differentiating and visualizing the two types of rings. Under the SEM the microstructure of the two classes of rings (translucent and opaque) was revealed; translucent rings were composed of narrow increments that were often characterized by discontinuities and irregularities, whereas the wider opaque rings were formed by thicker more consistently patterned increments.

The translucent zones with thin discontinuous increments were probably caused by periods of low growth in response to either environmental or physiological stress (Pannella, 1980). In taape, periods of slow growth often resulted in the formation of 70–90 very thin increments, with an average width of 0·8 μm in juvenile fish (S.D. 0·45 μm) and an average thickness of 0·4 μm (S.D. 0·30 μm) in mature fish [Fig. 1(a),(b)]. In contrast, daily increments laid down during periods of rapid growth were thicker. At these times the mean width of increments was 2·15 μm (S.D. 1·05 μm) in juvenile fish and 1·2 μm (S.D. 0·65 μm) in adult fish. These were arranged in higher-order rhythmical growth patterns of 3, 7, 14, and 28 increments [Fig. 1(c)]. Transitions between the two growth phases were usually abrupt.

In some samples a small group of seven thin but well-marked increments was laid down in the midst of a fast-growth zone [Fig. 1(d)]. In others this sharply defined but narrow seven-increment group was located at the start of a slow-growth period.

To determine the periodicity of the translucent and opaque rings, the number of increments in one presumptive annual period (one fast and one slow growth ring)

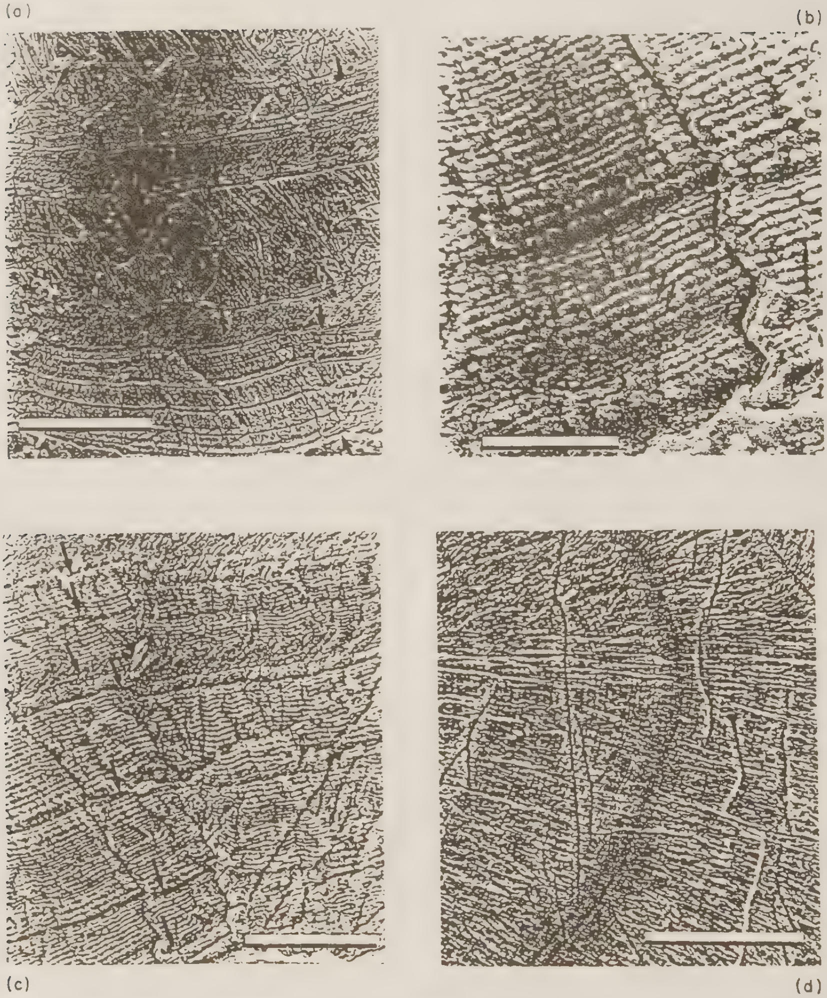

FIG. 1. Scanning electron micrographs of a taape otolith showing (a) fast (between arrows) and slow growth zones (scale bar = 75 μm), (b) thin increments (arrows) composed of discontinuous units (small arrows) and continuous units, laid down during a slow growth period (scale bar = 7·5 μm), (c) higher-order periodical growth patterns (arrows) (scale bar = 20 μm), and (d) thin increments standing out in a regular growth pattern (scale bar = 30 μm).

were enumerated. The mean number of increments was not significantly different from the number of days in a year (mean = 363, S.D. = 20·3, $t = 0{\cdot}1220 < t_{0{\cdot}05}$, d.f. = 15).

The occurrence of opaque margins on the otoliths (corresponding to periods of fast growth) was greatest during March (Fig. 2). As the spawning season advanced and the incidence of mature gonads increased, opaque margins became less evident in our samples, and there was an apparent slowing of growth. Although our samples were taken during only a portion of the year (March–October), and

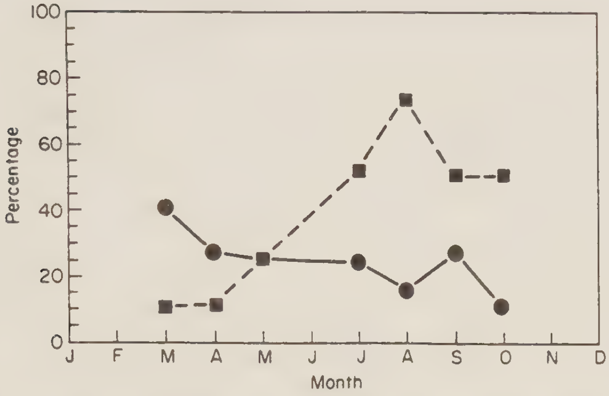

FIG. 2. Alteration of the taape otolith margin over the period of study, showing the monthly percentage of otoliths with opaque margins (% opaque, ●———●). Also shown is the seasonal representation of maturing females (% mature, ■— —■).

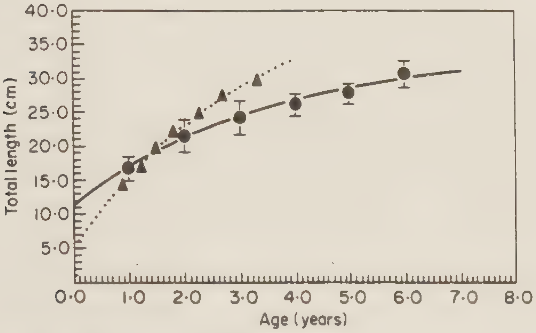

FIG. 3. Estimated von Bertalanffy growth curves obtained from the study of taape otolith annual marks (———) and increment microstructure widths (. . . .). Error bars represent ± 1·0 S.D.

opaque margins were sometimes difficult to detect due to translucency of the otolith, these data are consistent with the hypothesis that one opaque and one translucent ring were formed per year, i.e., the marks were annuli. Moreover, the data suggest that the opaque ring began to form at some time between November and March.

Once the annual periodicity of the rings was verified, the age of the fish was determined by enumerating the marks and considering 1 July as the standard birthdate. The resulting relationship between age and length is shown in Table I. These data were fitted to the von Bertalanffy equation and the growth parameters estimated (Fig. 3; Table II).

The size of the 31 otoliths sectioned and measured for increment widths was well correlated with body size. A double logarithmic regression relating otolith length

TABLE I. Hawaiian *Lutjanus kasmira* age–length relationship obtained by reading hyaline/opaque zones in otoliths

Total length (cm)	Age class (years)					
	1	2	3	4	5	6
13	1					
14	1					
15	3					
16	5					
17	2	3				
18	6	6				
19	3	4	2			
20		14	2			
21		10	3			
22		7	4			
23		11	6	1		
24		6	7	3		
25		7	10	3	1	
26			5	5		
27		2	1	2	2	1
28			4	4	2	
29			2	1	1	1
30					1	1
31						2
32						1
33						2
N	21	70	46	19	7	8
$\overline{\text{T.L.}}$	16·7	21·5	24·2	26·1	27·7	30·8

and T.L. was significant ($r^2 = 0{\cdot}83$), allowing prediction of T.L. from the radial length of the otolith (Fig. 4).

A total of 1915 estimates of otolith growth rate were obtained from measuring daily increment widths. These data were collected at otolith lengths as large as 6250 µm. Otolith growth rate rose rapidly, followed by a slow decline as otolith length increased (Fig. 5). Growth rate variance was roughly proportional to the square of the mean, a result used in developing statistical weights for each estimate of T.L. at age (Ralston & Williams, 1989).

A full summary of otolith growth by 500-µm intervals in otolith length is presented in Table III. The radial length of the otolith upon completion of growth through an interval was used to predict the corresponding T.L. with the regression presented in Fig. 4. To avoid extrapolating the regression to otolith lengths smaller than those actually measured, predictions were made only for otolith lengths greater than 3000 µm. The resulting length-at-age data were fitted to the von Bertalanffy equation and the growth parameters estimated (Fig. 3; Table II).

The available data on taape growth in the Mariana Islands and American Samoa, determined by the same increment width method (Ralston & Williams, 1988*a*,*b*), proved to be significantly different from taape growth rate in Hawaii (Table IV).

TABLE II. Growth parameters of Hawaiian *Lutjanus kasmira* estimated from otoliths and length frequency analysis

Method	Sample	L_∞ (cm)	K (year^{-1})	t_0 (years)
Otoliths				
Annual rings	1987	34·0	0·29	−1·37
Increment width	1987	42·9	0·33	−0·37
Length frequency				
Wetherall *et al.*	1987	32·3	—	—
	1978/79	24·1	—	—
	pooled	32·3	—	—
ELEFAN I	1987	33·0	0·67	—
	1978/79	24·8	0·29	—
	pooled	28·1	0·37	—
ELEFAN V	1987	29·9	0·41	—
	1978/79	23·6	0·63	—
	pooled	28·9	0·34	—

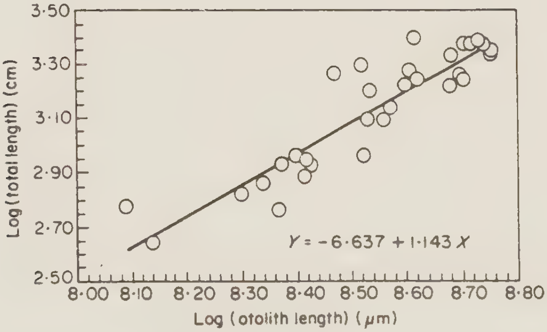

FIG. 4. The relationship between taape otolith size (radial length from focus to postrostrum) and total fish length.

LENGTH–FREQUENCY ANALYSIS

The length ranges sampled by the two different fishing gears (gill net and hook-and-line) were very different. In shallow water, only small fish were caught, while in the hook samples from deep water the fish were substantially larger (Fig. 6). Moreover, the 1979 gill net sample showed a substantial increase in the number of fish in the smallest length categories, relative to the 1978 net sample; this suggests that a major recruitment episode occurred in shallow water during early winter.

Estimates of L_∞ were obtained by application of the regression method of Wetherall *et al.* (1987) to the length–frequency data (Table II). Due to the absence

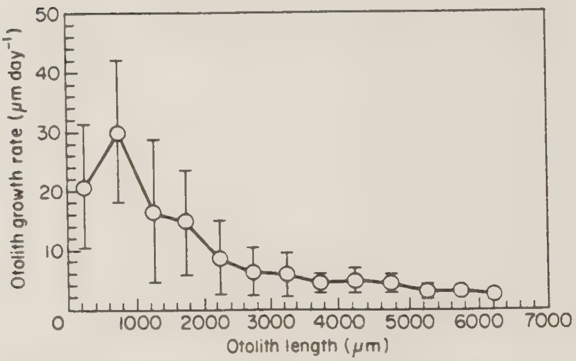

FIG. 5. Relationship between taape otolith growth rate and otolith length in 500-μm intervals.

TABLE III. Summary of otolith length, otolith growth rate, mean age, and total length for Hawaiian *Lutjanus kasmira*

Otolith length interval (μm)	*N*	Mean otolith growth rate (μm day^{-1})	Interval duration (days)	Age (years)	Predicted total length (cm)	Statistical weight
0–500	146	20·83	24·0	0·066	—	—
500–1000	45	30·10	16·6	0·111	—	—
1000–1500	126	16·59	30·1	0·194	—	—
1500–2000	166	14·72	34·0	0·287	—	—
2000–2500	159	8·66	57·7	0·445	—	—
2500–3000	181	6·34	78·9	0·661	—	—
3000–3500	124	5·77	86·7	0·898	14·8	1·00
3500–4000	99	4·39	113·9	1·210	17·2	0·97
4000–4500	270	4·85	103·1	1·492	19·7	0·95
4500–5000	226	4·24	118·0	1·815	22·2	0·94
5000–5500	183	3·08	162·4	2·260	24·8	0·93
5500–6000	157	3·12	160·3	2·699	27·4	0·91
6000–6500	33	2·37	211·3	3·277	30·0	0·90

of large fish in the shallow-water gill net samples taken in 1978/79, the estimate of L_∞ obtained with these data was lower (24·1 cm T.L.) than for either the 1987 deep-water hook-and-line sample alone or the entire pooled length–frequency data set (32·3 cm T.L.).

Regression method estimates of L_∞ were then used as starting points for the ELEFAN I procedure. Parameter estimates obtained with ELEFAN I varied considerably, depending on which data were used (Table II). Final values of L_∞ ranged from 24·8 to 33·0 cm T.L., whereas estimates of K ranged from 0·29 to 0·67 year^{-1}.

Table IV. Results of the multivariate test between measured growth of taape in Hawaii, in American Samoa and in Mariana Archipelago. Entries include the pooled, estimated, variance-covariance matrix (S) and its inverse (S-1), the calculated T^2 statistic and the critical F_0

Hawaii-Samoa							
S	8·103823	−0·16625	−0·70014	S-1	7·76461	560·8541	−44·7389
	−0·16625	0·00359	0·01626		560·854	43083·31	−3739·08
	−0·70014	0·01626	0·08244		−44·7389	−3739·08	370·063
$P_1 - P_2 =$ i10·05		0·0442	1·5728	$F_0 = 2·605$			
					$T^2 = 347·9052$		
Hawaii-Mariana							
S	19·6352	−0·47458	−2·46353	S-1	−0·00992	−0·1402	−0·4581
	−0·4735	0·00256	0·00944		−0·16219	1271·3	−245·67
	2·4635	0·00951	0·05050		−0·45380	−246·03	43·676
P_1-P_2=i–12·7		0·215	1·686	$F_0 = 2·605$			
					$T^2 = 23·4335$		

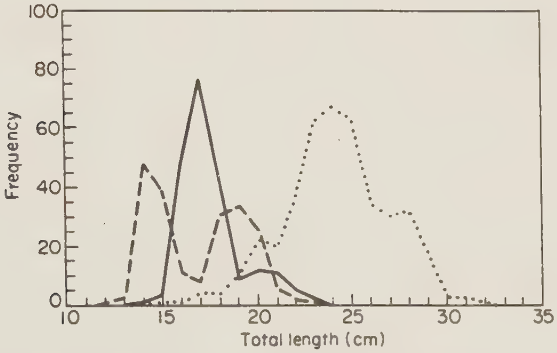

Fig. 6. Taape length frequency distributions. The 1978 (———) and the 1979 (— —) samples were obtained in shallow water (15 m) with gill nets. The 1987 sample (. . .) was drawn from deep water (40 m) with hook-and-line gear.

Reconstructed annual growth rates were derived for the joint analysis of length–frequency and otolith data. These were restricted to lengths appropriate to the length–frequency data used (i.e. T.L. ≤ 23 cm for the gill net samples obtained in 1978/79). Under this constraint, the ELEFAN V program produced estimates of the von Bertalanffy growth parameters given in Table II. As with the other length–frequency analyses, the 1978/79 data produced the lowest estimate of L_∞ (23·6 cm T.L.) and, correspondingly, the estimate of K was the highest (0·63 year^{-1}).

The growth performance index ($\varphi = \log_{10} K + \{2^*\log_{10} L_\infty\}$) (Pauly & Munro, 1983) was calculated for each for the eight entries in Table II where both the K and L_∞ parameters were estimated. Values ranged from 2·25 (ELEFAN I applied to the 1978/79 sample) to 2·86 (ELEFAN I applied to the 1987 sample), with a mean of $\varphi = 2{\cdot}55$ and S.D. = 0·19.

IV. DISCUSSION

The opaque and translucent rings found in taape otoliths were laid down with annual periodicity, allowing age determination with relative ease. Examination of otolith microstructure by SEM revealed the existence of very thin (0·4 µm) bipartite growth increments that, due to their small size, were below the resolving threshold of a light microscope (Campana *et al.*, 1987; Jones & Brothers, 1987). The narrow translucent rings deposited during periods of slow growth were largely composed of these very thin increments. Therefore, translucent slow growth regions did not display a full complement of increments when viewed with a light microscope.

The increment width method (Ralston & Miyamoto, 1983; Ralston, 1985; Ralston & Williams, 1989) is based upon measuring the widths of daily increments at specific sites along a predefined axis of otolith growth. In theory, all daily increments, from focus to otolith margin, need not be visible to employ this technique. Although regions of the otolith characterized by ill-defined microstructure have previously been attributed solely to preparation defects (Ralston, 1985), these areas can also occur when increments are so small that they cannot be resolved with a conventional light microscope (Campana *et al.*, 1987; Jones & Brothers, 1987). In this situation, a sample of increment widths obtained by light microscopy would not be representative, resulting in the overestimation of otolith growth rates (Table III) and the underestimation of age. This kind of error may explain the discrepancy (Fig. 3) between estimates of asymptotic length (34·0 *v.* 42·9 cm T.L.) and growth coefficient (0·29 *v.* 0·33 year^{-1}) derived from the two methods of otolith analysis.

Mizenko (1984) also used a light microscope in his study of *L. kasmira* otoliths from Western Samoa, and reported the existence of regions lacking clear increment microstructure. Increments smaller than 0·8 µm (the practical limit of resolution with light microscopy) are not uncommon in tropical species (Morales-Nin, 1988). These findings illustrate the advantage of previewing otolith microstructure with SEM before attempting to age tropical species with a light microscope. If the latter is effective at resolving the smallest daily increments, one can proceed using either whole counts or the increment width method.

As an alternative approach, Ralston & Williams (1988*a*, 1989) advocated use of the regression method of Wetherall *et al.* (1987) to estimate the L_∞ parameter of the von Bertalanffy growth equation. Increment widths obtained from juvenile stages, where microstructure is more easily resolved, can then be used to estimate K and t_0, constrained by the estimated value of L_∞ obtained from the regression method.

Analysis of length–frequency data showed that parameter estimates were strongly affected by which sample was analysed. The pooled data produced results most similar to those obtained with otoliths, although in this situation the goodness-of-fit of the ELEFAN I program was poor (ESP/ASP = 0·110). The fit was much better when independently-obtained otolith growth rates were incorporated into the calculations of ELEFAN V (ESP/ASP = 0·437). These findings indicate that if a species has a bathymetric and/or geographical distribution that is heterogeneous with respect to length structure (e.g. Fig. 6), length–frequency samples may not be representative of the whole population. The difficulty is knowing when this occurs and correcting for it.

The estimation of growth in tropical marine fish has long been considered problematic due to the supposed lack of annual rings in their hard structures and their 'continuous' spawning which was assumed to render impossible the analysis of the growth of tropical fish based on the study of length–frequency data. Although biological and environmental conditions combine to make taape age and growth determination difficult, the multi-approach used herein made it possible to determine age and growth avoiding the subjectivity generally involved in age interpretation.

The presence of daily growth rings in the otoliths is, presumably, related to the diurnal changes in taape activity levels. Taape feed actively in rocky areas at night, while staying in sandy shallower areas at day (J. D. Parrish pers. comm.). These daily activity levels might be related to concomitant changes in the oxygen budget of the tissues. Thus, high activity levels during feeding, sustained high-speed swimming etc. will induce changes in the fluids surrounding the otoliths, and must result in alterations of the chemistry of the outermost layer of the otolith. Probably the discontinuous increment layer is laid down during the activity periods.

Seasonal growth cycles in tropical fish might be related to physiological changes induced by the influence of temperature, feeding regime and reproductive cycle. The evidence presently available suggests that a seasonal temperature difference of 2–3° C might be sufficient to cause ring formation (Morales-Nin, in prep.). The Hawaii nearshore marine system shows small temperature fluctuations which might be related to changes in taape growth rate. Seasonal changes in feeding regime do not seem evident in taape (Oda & Parrish, 1981), while the reproductive cycle appears to be related to the ring formation (Fig. 2). During the maturity period the metabolic energy seems to be diverted from growth, causing the formation of thin increments which are in turn reflected in hyaline seasonal growth rings.

Growth of taape in the Hawaiian Islands is rapid in comparison to the Mariana Islands (Ralston & Williams, 1988*a*) where the species is indigenous. Our estimates of growth rate are similar to those obtained in New Caledonia by Loubens (1980) and in American Samoa by Ralston & Williams (1988*b*). Moreover, our calculations of growth performance index indicate that taape is, relatively speaking, a fast-growing species of snapper (Manooch, 1987).

Taape in Hawaii shows a growth rate superior to that (K year^{-1} = 0·146) of the deep-water Hawaiian lutjanid *Pristipomoides filamentosus* (Ralston & Miyamoto, 1983). The very successful introduction of taape into the Hawaiian nearshore marine ecosystem, which had been entirely lacking in snappers and groupers, may have been due to its fast growth rate which, in turn, might have been enhanced by a lack of close competitors and predators.

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References

Bernard, D. R. (1981). Multivariate analysis as means of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* **38,** 233–236.

Brey, T. & Pauly, D. (1986). Electronic length–frequency analysis: a revised and expanded user's guide to ELEFAN O, 1 and 2. *Ber. Inst. Meeres.* Christian-Albrecht Univ. Kiel. No. 149. 76 pp.

Brothers, E. B. (1980). Age and growth studies on tropical fishes. In *Stock Assessment for Tropical Small-scale Fisheries* (S. B. Saila & P. M. Roedel, eds), pp. 119–136. Kingston, RI: International Center for Marine Resource Development, University of Rhode Island.

Campana, S. E., Gagné, J. A. & Munro, J. (1987). Otolith microstructure of larval herring (*Clupea harengus*): image or reality? *Can. J. Fish. Aquat. Sci.* **44,** 1922–1929.

Jones, C. & Brothers, E. B. (1987). Validation of the otolith increment aging technique for striped bass, *Morone saxatilis*, larvae reared under suboptimal feeding conditions. *Fish. Bull., U.S.* **85,** 171–178.

Loubens, G. (1980). Biologie de quelques especes de poisson du lagon néo-Calédonien. I. Détermination de l'age (otolithométrie). *Cah. ORSTOM, Sér. Océanogr.* **16**(3 and 4), 263–283.

Manooch, C. S., III (1987). Age and growth of snappers and groupers. In *Tropical Snappers and Groupers: Biology and Fisheries Management* (J. J. Polovina & S. Ralston, eds), pp. 329–374. Boulder, CO: Westview Press, Inc.

Mizenko, D. (1984). The biology of western Samoan reef-slope snapper (Pisces: Lutjanidae) populations of : *Lutjanus kasmira, Lutjanus rufolineatus*, and *Pristipomoides multidens*. Unpubl. M.S. thesis, Univ. Rhode Island. 66 pp.

Morales-Nin, B. (1988). Caution in the use of daily increments for ageing tropical fishes. *Fishbyte (ICLARM)* **6**(2), 5–6.

Morgan, G. R. (1987). Incorporating age data in length-based stock assessment methods. In *Length-based Methods in Fishery Research* (D. Pauly & G. Morgan, eds), pp. 137–146. ICLARM Conference Proceedings 13. Manila, Philippines: International Center for Living Aquatic Resource Management.

Oda, D. & Parrish, J. D. (1981). Ecology of commercial snappers and groupers introduced to Hawaiian reefs. In *The Reef and Man* (E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr. & R. T. Tsuda, eds), pp. 59–67. Proceedings of the Fourth International Coral Reef Symposium Vol. 1. Quezon City, Philippines: Marine Science Center, University of the Philippines.

Pannella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science, Washington DC* **173,** 1124–1127.

Pannella, G. (1980). Growth patterns in fish sagittae. In *Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change* (D. C. Rhoads & R. A. Lutz, eds), pp. 519–560. New York: Plenum Press.

Pauly, D. & Gaschutz, G. (1979). A simple method for fitting oscillating length growth data, with a program for pocket calculator. *ICES CM 1979*/G:24. 26 pp. (mimeo.).

Pauly, D. & Munro, J. L. (1983). Once more on the comparison of growth in fish and invertebrates. *Fishbyte (ICLARM)* **2**(1), 21.

Ralston, S. (1985). A novel approach to aging tropical fish. Int. Center Living Aquat. Resour. Mgmt Manila, Philippines, *ICLARM Newsletter* **8**(1), 14–15.

Ralston, S. & Miyamoto, G. T. (1983). Analysing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. *Fish. Bull., U.S.* **81,** 523–535.

Ralston, S. & Williams, H. A. (1988*a*). Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. *U.S. Dept Commerce, NOAA Tech. Memo NMFS, NOAA-TM-NMFS-SWFC-113.* 47 pp.

Ralston, S. & Williams, H. A. (1988*b*). Age and growth of *Lutjanus kasmira, Lethrinus rubrioperculatus, Acanthurus lineatus*, and *Ctenochaetus striatus* from American Samoa. *Southwest Fish. Cent. Honolulu Lab., Natl Mar. Fish. Serv., NOAA, Admin. Rep. H-88-18*. 11 pp.

Ralston, S. & Williams, H. A. (1989). Numerical integration of daily growth increments: an efficient means of aging tropical fishes for stock assessment. *Fish. Bull., U.S.* **87**(1), pp. 1–16.

Randall, J. E. (1960). New fishes for Hawaii. *Sea Frontiers* **6**, 33–43.

Wetherall, J. A., Polovina, J. J. & Ralston, S. (1987). Estimating growth and mortality in steady state fish stocks from length–frequency data. *Length-based Methods in Fishery Research* (D. Pauly & G. Morgan, eds), pp. 53–74. ICLARM Conference Proceedings 13. Manila, Philippines: International Centre for Living Aquatic Resource Management.

Williams, T. & Bedford, B. C. (1974). The use of otoliths for age determination. In *The Ageing of Fish* (T. B. Bagenal, ed.), pp. 114–123. Old Woking, Surrey: Unwin Brothers.

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The Weddell-Scotia Confluence in Midwinter

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The southern central Scotia Sea, site of the Weddell-Scotia Confluence where outflowing Weddell Sea waters converge with the eastward flowing waters of the Scotia Sea, was sampled during June–August (austral winter) 1988 with respect to temperature and salinity. Both drogued and ice-mounted drifters, tracked by Argos, were deployed in the region and yielded Lagrangian drift tracks of ice and water motion. The data substantiate past accounts of the region, based upon summer field research, as dominated by eastward flow upon which a complex array of mesoscale features is superimposed. Weddell-Scotia Confluence Water, documented by past summer work in the region and characterized by decreased static stability, was not detected, and the Scotia Front was not well defined. The region was one of intense mixing activity and primarily anticyclonic mesoscale features. Two such features, one an eddy and the other either an eddy or a meander in the Scotia Front, dominated the mesoscale field. With warm cores and containing Polar Front Water, they may have been advected eastward from Drake Passage or may have formed as detached eddies from a sharp northward bend in the Polar Front which typically lies just west of the study region. Several smaller eddies, primarily anticyclonic and some having warm cores, were also detected. There was no evidence of the deep convective mixing which has been hypothesized, on the basis of past summer data, to occur in winter, and vigorous vertical mixing was limited to a 100-m-thick upper mixed layer. Vertical stability in the upper layers was enhanced by low-salinity water derived from melting ice. Temperature-salinity analyses show that winter water in the study region can be derived through isopycnal mixing between waters from the Scotia Sea and waters from the northwestern Weddell Sea. This is in apparent contrast with summer conditions, wherein conditioning of water either through vertical mixing or via lateral mixing on continental margins has been invoked to arrive at the water mass characteristics which typify the Weddell-Scotia Confluence.

1. INTRODUCTION

In this paper we present physical oceanographic results from an austral winter 1988 field study in the southern central Scotia Sea. This study was part of the Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIEZ) program, which has addressed the ecosystem associated with the Antarctic marginal ice zones [cf. *Nelson et al.*, 1987, 1989].

Scotia Sea circulation is dominated by eastward to northeastward flow associated with the Antarctic Circumpolar Current (ACC). Hydrographic conditions reflect the presence of water masses from the Bellingshausen and Weddell seas, Bransfield Strait, and the ACC. Water from Bransfield Strait and from the westernmost Weddell Sea may reflect modification by cooling, freshening, and mixing during its passage over the continental shelf surrounding the Antarctic Peninsula. Bellingshausen Sea and ACC waters, which enter the region via Drake Passage, comprise Scotia Sea Water. Weddell Sea Water enters the region from the northwestern Weddell Sea over the South Scotia Ridge, through the gaps west and east of the South Orkney Islands.

The transitional region in which Scotia Sea and Weddell Sea waters converge and mix is called the Weddell-Scotia Confluence (WSC). It is the site of an additional water type, which cannot be derived through mixing among the source waters but must rather originate through conditioning of the inflowing Weddell Sea and Bransfield Strait waters, called Weddell-Scotia Confluence (WSC) Water. Descriptions of this region have been provided by *Deacon and Moorey* [1975], *Deacon and Foster* [1977], *Gordon et al.* [1977], *Patterson and Sievers* [1980], and *Gordon* [1988].

The WSC dominates the oceanography of the southern Scotia Sea in summer. This zonally oriented, elongate feature, which has been observed to vary in width from a few tens of kilometers [*Deacon and Foster*, 1977] to several hundred kilometers [*Gordon et al.*, 1977; *Patterson and Sievers*, 1980], coincides along its axis roughly with the South Scotia Ridge. Bounded over at least part of its extent on the north and south by the Scotia and Weddell fronts, respectively, waters in the WSC tend in summer to be colder and less statically stable than those to the north and south. The locally decreased stability is due to increased upper layer and decreased lower layer salinity.

The weak summer stratification in the WSC has led previous investigators to postulate that the southern Scotia Sea is a site during winter for deep vertical mixing driven by cooling and brine rejection consequent to sea ice formation. The winter marginal ice zone traverses the Scotia Sea zonally, roughly coincident with the WSC (as defined using summer data), from about June to October [*Zwally et al.*, 1983; *Comiso and Zwally*, 1989]. Hence it has generally been assumed that convection might be abetted by the strong sea-air temperature differences which typify winter marginal ice zones in general. *Deacon and Moorey* [1975] speculated

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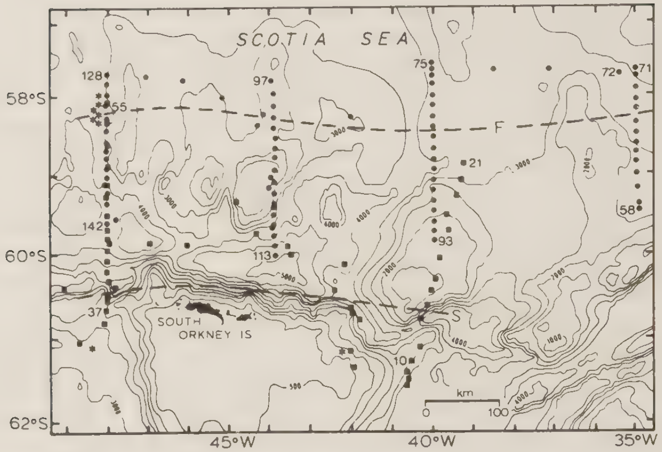

Fig. 1. Geographical location of the study region in the southern Scotia Sea. Locations for CTD casts are indicated by squares (leg 1) and circles (leg 2). Approximate locations for the ice edge at the start and at the finish of the program are shown by the two dashed curves labeled S and F, respectively. Asterisks indicate approximate drifter release sites. Station numbers show the ends of plotted vertical profiles, transects, and θ-S curves which are referred to specifically in other figures. Bathymetry is courtesy of B. A. Huber of Lamont-Doherty Geological Observatory, and depths are in meters.

that the combined high surface salinity and weak stratification might be remnants of vigorous vertical mixing through winter convection. *Patterson and Sievers* [1980] suggested, alternately, that the reduced stratification is due to oceanic lateral boundary layer mixing processes acting on Bransfield Strait and Weddell Sea waters in the continental boundary regions farther west, coupled with admixture of meltwater. There have been no published winter data obtained from the region prior to the study reported in this paper; therefore it has not been possible to estimate the extent to which the summer data represent year-round conditions or the extent to which deep winter convection may in fact occur.

The 1988 field program acquired temperature, salinity, and Lagrangian current data from the southern Scotia Sea region during midwinter. This paper describes and discusses these results. Field methods are described in section 2. The observations are described in section 3 and discussed in section 4.

2. THE FIELD PROGRAM

The winter 1988 Scotia Sea field work was carried out in two successive legs from the Universities National Oceanographic Laboratories System (UNOLS) vessel Polar Duke. Leg 1 took place from June 9 to July 5 while the seasonal ice edge was still migrating northward toward its maximum extent. Activities during this leg focused on the immediate vicinity of the ice edge and southward into the multiyear pack ice. Temperature and salinity data were obtained on two relatively rapid transects (less than 72 hours each required for completion), using a shipboard conductivity-temperature-depth profiling system (CTD), nominally along 48°W and 40°W and in a loose grid which fell mostly between these transects (Figure 1). Nominal station spacing along the transects was 15 km. Leg 2 took place from July 18 to August 13 and encompassed the period over which the ice edge attained its maximum northward extent. Leg 2 emphasized water column measurements in and north of the ice edge, and transects having stations spaced nominally 15 km apart were occupied along 48°W, 44°W, 40°W, and 35°W (Figure 1). Individual meridional transects were occupied as rapidly as possible, each in less than 48 hours for leg 2. However, significantly longer periods elapsed between occupations of transects, as indicated by the dates given in the figure legends for each transect.

The CTD observations were carried out using a Sea Bird model SBE 9/11 profiling system. The sampling rate was 12 Hz on all casts. The lowering rate for the underwater unit was approximately 0.5 m/s for the upper 200 m and 1.0 m/s at greater depths. A hardware problem with the CTD limited data acquisition during the first part of leg 1 (including the first transect along 40°W) to depths shallower than 200 m and compromised the quality of salinity data on the later part of this leg. This problem was corrected prior to leg 2. The CTD temperature and salinity sensors were calibrated prior to and following the field work at the Northwest Regional Calibration Center in Bellevue, Washington. There were no significant differences between the two resulting sets of calibration values. The performance of the conductivity sensor was monitored during the field work by carrying out salinity analyses on rosette-derived water samples every third or fourth cast using a Plessey "suitcase" laboratory salinometer. The final data, excluding those salinity data obtained during the later part of leg 1, are accurate to within 0.01°C in temperature and 0.01 psu (practical salinity unit; 1 psu = 1‰ salt by weight) in salinity.

Two Polar Research Laboratories (PRL) (Carpinteria, California) Argos-tracked automatic data acquisition and position (ADAP) units were deployed early in leg 1 on ice floes in the southern portion of the study area (Figure 1). The first of these did not survive long enough to provide signifi-

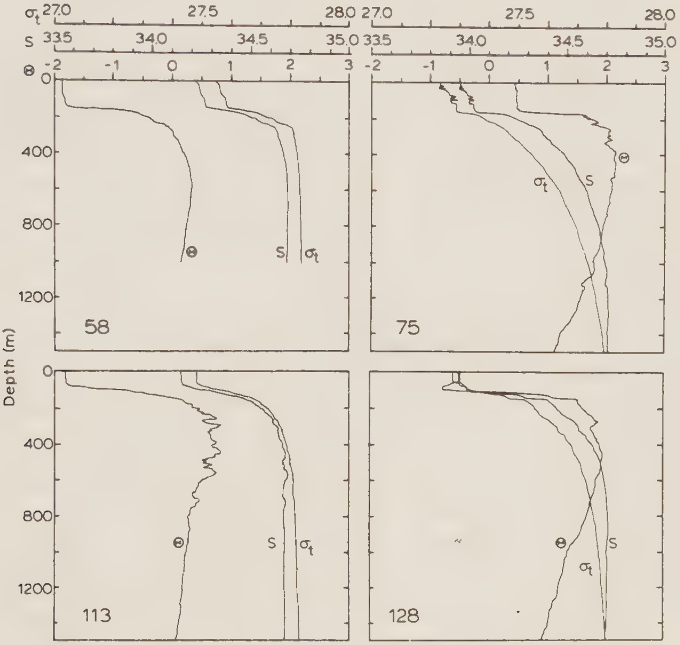

Fig. 2. Representative vertical profiles of potential temperature θ (degrees Celsius), salinity S (psu), and density σ_t. Cast numbers are at the bottom left of each set of profiles, and cast locations are shown on Figure 1.

cant ice drift information. The second survived throughout the field program. Six Argos-tracked, surface-drogued Tristar drift buoys (Technocean, San Diego, California) were deployed at the start of leg 2 along 48°W in the northwest corner of the study area (Figure 1). Three of these provided useful drift tracks, while three ceased to transmit too soon after deployment to provide records. The drift buoys with short survival times were probably destroyed by sea ice, which advanced rapidly because of off-ice winds directly following the buoy deployments.

3. OBSERVED CONDITIONS

3.1. *Hydrographic Conditions*

The regional vertical temperature, salinity, and density characteristics are summarized (Figures 2–11) as representative vertical profiles, as horizontal distributions, and as vertical distributions along transects.

3.1.1. *Horizontal and isopycnal distributions.* The southern Scotia Sea was typified by a relatively cold (−1.8°–1.0°C) upper layer of order 100 m in depth (Figure 2). It was usually, but not always, vertically homogeneous; at some locations more than one layer was present. The upper layer was underlain by a region of strong vertical gradients in temperature, salinity, and density. Below this gradient zone lay a warmer layer comprised of the Circumpolar Deep Water (CDW), having maximum temperatures which exceeded 2.0°C near 400 m depth in the northern part of the study area.

The distributions of temperature and salinity at 50 m depth are assumed to represent the upper mixed layer (Figure 3). South of the −1.75°C isotherm (58°30′–59°00′S) the upper layer was effectively at the freezing point (below −1.80°C) and had salinities of 34.0–34.2 psu. Warmer patches were present at about 59°S on 48°W and 40°W. North of the −1.75°C isotherm, temperature increased irregularly northward along 48°W and 40°W to the relatively warm patches of water (>1.0 and >0.0°C, respectively) at the northern ends of the transects. Temperatures increased less markedly (from the freezing point to more than −1.5°C) along 44°W and 35°W. Salinity decreased only weakly northward, from 34.0–34.2 to 34.0–34.1 psu, and exhibited considerable scatter. Slightly lower salinities (<34 psu) were associated with the warm patches at the northern ends of the 48°W and 40°W transects.

The 400-m level was selected because this was the approximate depth of the CDW temperature maximum (Figure 4). Temperature at this depth increased from $T < 0.5$°C in the south northward to more than 2°C. A cold (less than −0.5°C) patch was present at about 58°30′S on 48°W, and warm patches were observed near the southern end of the 48°W transect and the northern end of the 35°W transect. Warm (>2.0°C) patches at the northern ends of the 48°W and 40°W transects coincided with elevated temperatures and depressed salinities in the upper layer (Figure 3).

These horizontal temperature and salinity distributions can be compared with results from previous work. *Foster and Middleton* [1984, Figure 5] plotted potential temperature at the 50-dbar level. They depict a strong upper layer thermal front about 100 km north of the South Orkney Islands. Our

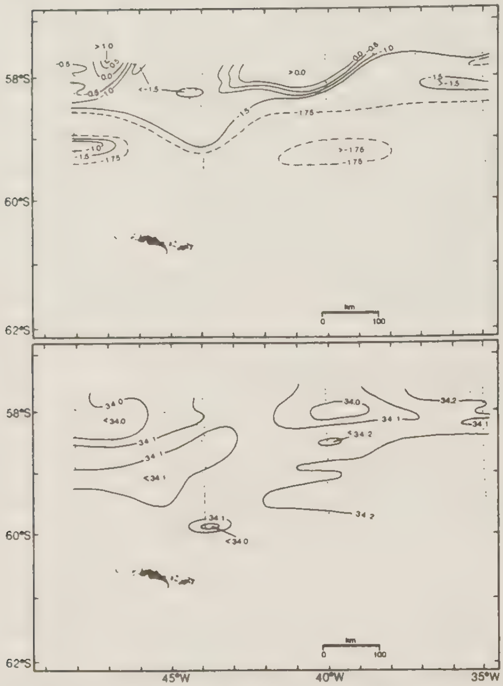

Fig. 3. Distributions of (top) temperature (degrees Celsius) and (bottom) salinity (psu) at 50 m during leg 2, July 18 to August 13, 1988.

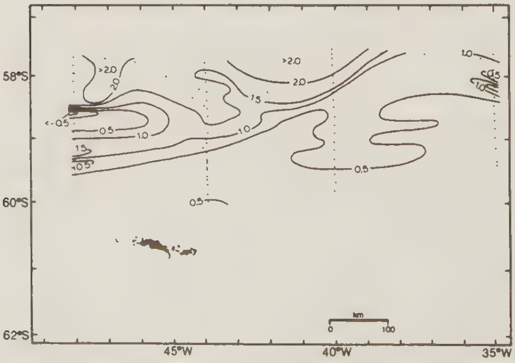

Fig. 4. Distribution of temperature (degrees Celsius) at 400 m during leg 2, July 18 to August 13, 1988.

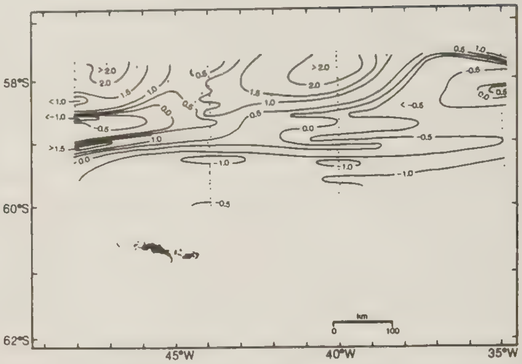

Fig. 5. Distribution of temperature (degrees Celsius) on the σ_t = 27.62 isopycnal surface during leg 2, July 18 to August 13, 1988.

winter data do not show such a feature, but they may not have extended far enough south to detect its presence. Foster and Middleton also noted the similarity of horizontal temperature patterns with increasing depth in summer data and suggested that the related features had developed about vertical axes. Both *Gordon et al.* [1977] and *Patterson and Sievers* [1980] have stated, on the basis of summer data, that the WSC is a site of significantly elevated upper layer salinity compared with waters to the north and south. They showed surface salinities of order 34.3 psu in the WSC. Our winter data show surface salinities to be less, typically 34.1 psu. Hence the winter data do not show a well-defined salinity increase in the WSC over surrounding areas, as opposed to summer. *Deacon and Foster* [1977] suggested that winter cooling, brine rejection from freezing, and advection of Weddell Sea water into the region raise upper layer salinities in the WSC to more than 34.5 psu while lowering temperatures to the freezing point. While winter water temperatures were indeed near or at the freezing point, observed upper layer salinities were about 0.5 psu lower than predicted by Deacon and Foster. These differences will be discussed below (section 4).

The distribution of temperature is presented on the σ_t = 27.62 isopycnal surface (Figure 5). This surface was selected because it extended throughout the study area, deepening to more than 500 m in the warm (>2°C) patches along 48°W and 40°W to the north and shoaling to the bottom of the upper mixed layer in the south (see Figures 6–11). Temperature on this surface decreased from >2.0°C in the two northern warm patches to less than −1.0°C in the south. Greater complexity was present than for the temperature distribution at 400 m. Meridional gradients were qualitatively greater at 48°W than farther east and appeared to be associated with the two warm-core features along that transect. This pattern is consistent with formation of the frontal and other mesoscale features to the west and decay via lateral mixing processes as they progress eastward with the mean flow. *Patterson and Sievers* [1980] noted, in qualitative agreement with our observation, that the confluence and its associated fronts are quite well defined just off the Antarctic Peninsula where they are first formed, but that they become increasingly confused by mesoscale structures eastward from that point as they are advected downstream. *Foster and Middleton* [1984] noted that identifiable frontal structures were not present in the eastern Scotia Sea, but rather that the fronts had degenerated into a field of mesoscale eddies.

3.1.2. *Vertical distributions.* Vertical distributions of temperature, salinity, and density are presented for the meridional transects (Figures 6–11). These are presented sequentially starting with the westernmost transect, so that the distributions closest to the initial convergence of water

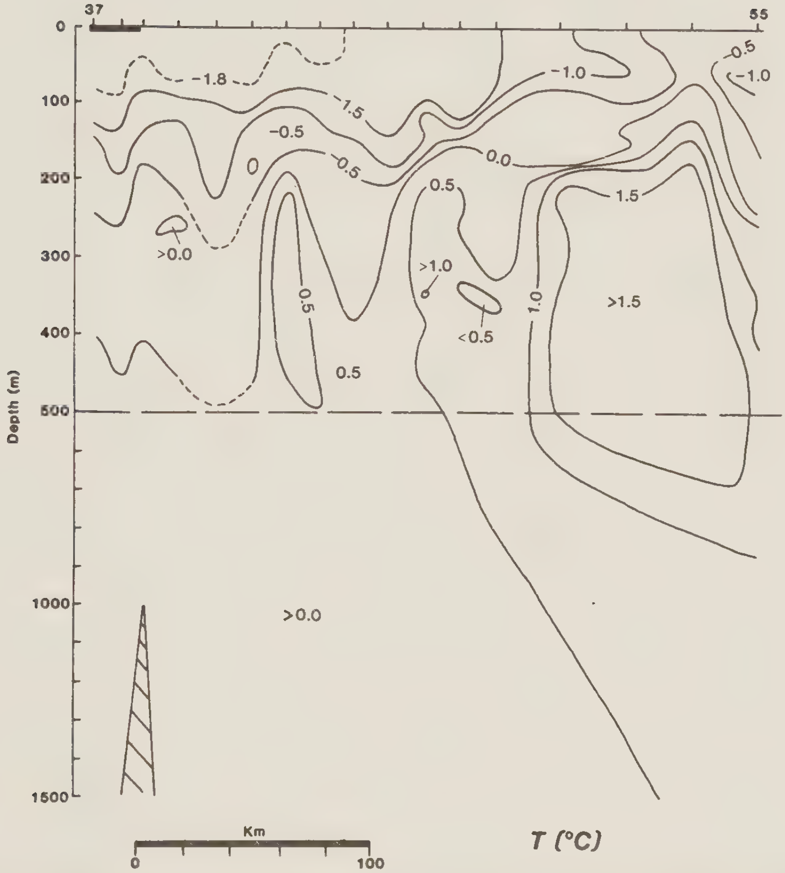

Fig. 6. Distribution of temperature (degrees Celsius) along 48°W during leg 1, July 2–5, 1988. Salinity (and derived density) data were unreliable along this transect because of hardware problems and are not presented (see text). For this and all subsequent transects the heavy line at the surface indicates sea ice cover, and the transect location is indicated in Figure 1.

types are presented first. Occupation of the 48°W transect during both leg 1 and leg 2 allows the comparison of temperatures at two different times. The transects occupied near and along 40°W on legs 1 and 2 did not coincide in space sufficiently to allow meaningful comparison.

Property distributions along the transects showed a cold upper layer, sometimes with low-salinity lenses, and a warm deep layer having maximum temperatures of 1.5°–2.0°C at 400- to 500-m depths in the northern portions. A weak salinity maximum was often present at the warm core, as shown, for example, by the 34.7-psu isohaline on three of the transects. Isopycnals sloped downward to the north in all the transects. This downsloping occurred primarily in the northern halves of the transects, consistent with a stronger baroclinic flow field in the northern than in the southern study region (see the discussion below on circulation, section 3.2). The strongest downward sloping occurred along 48°W and 44°W coincident with the southern edges of the warm-core features there.

There was no indication on the transects of deep-reaching vertical uniformity which may have reflected vertical mixing. The entire region appeared, conversely, to be well stratified in both temperature and salinity except for the relatively thin (compared to the overall water depth) upper mixed layer.

There was no indication that surface density (as σ_t) was elevated within the confluence by as much as 0.6 over Antarctic Zone surface values to the north, as reported by *Gordon et al.* [1977] on the basis of summer data. Rather, the winter surface densities varied from about 27.3 to 27.6 with the lower values typically being associated with the ice edge region. The lower densities tended to occur north of the ice edge, hence in the northern part of the study area. Along 44°W on July 31 to August 2, however, the surface density was 27.4 both north and south of the ice edge, showing little meridional change (Figure 8).

Property distributions along 48°W exhibited the greatest complexity, particularly with respect to temperature, seen

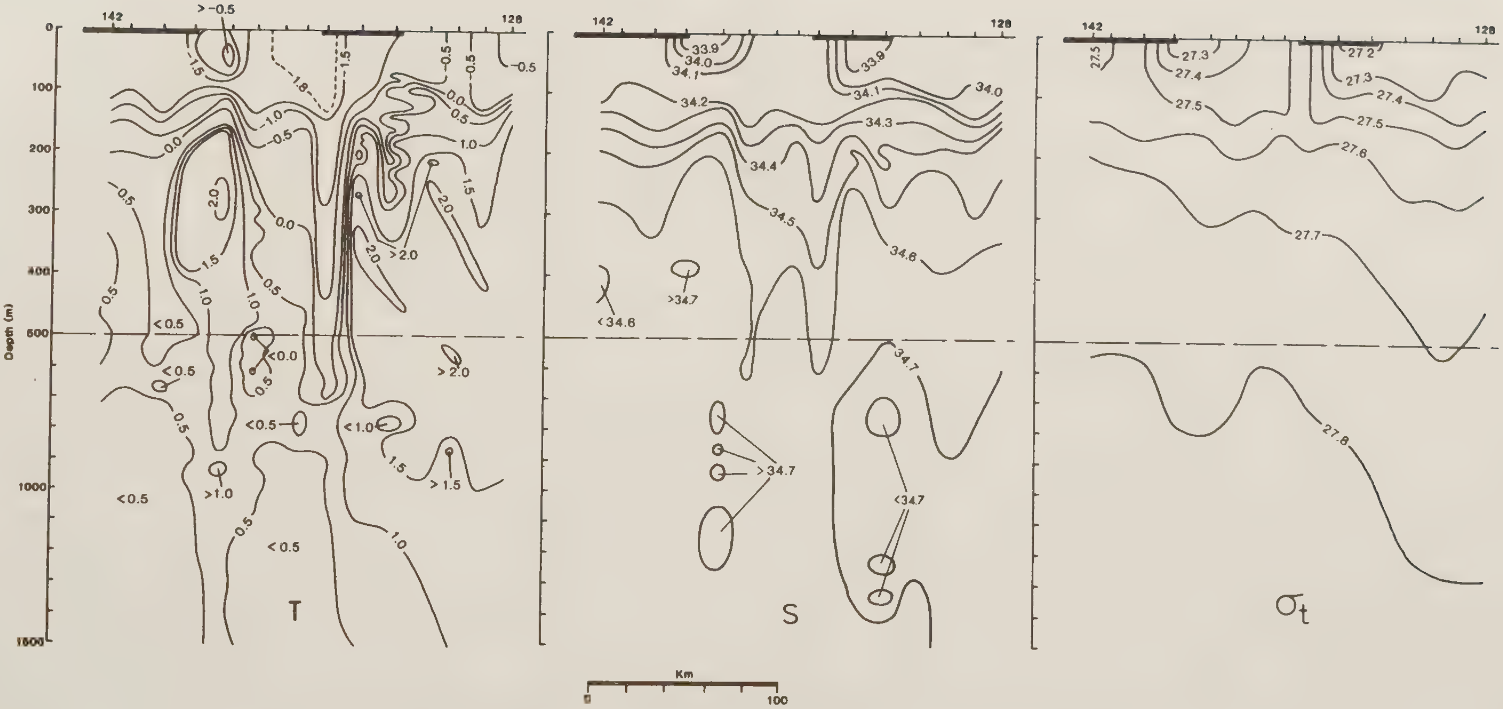

Fig. 7. . Distributions of temperature (degrees Celsius), salinity (psu), and density (as σ_t) along 48°W during leg 2, August 10–11, 1988.

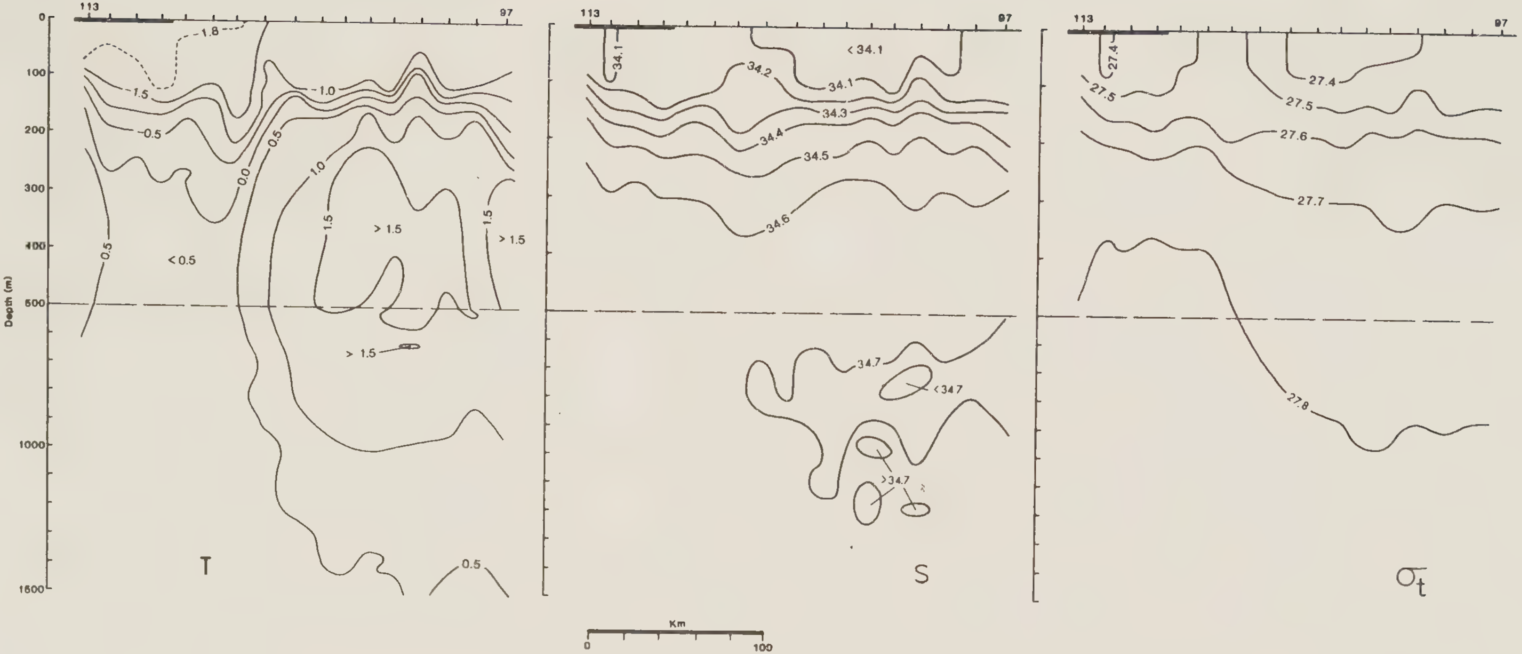

Fig. 8. Distributions of temperature (degrees Celsius), salinity (psu), and density (as σ_t) along 44°W during leg 2, July 31 to August 2, 1988.

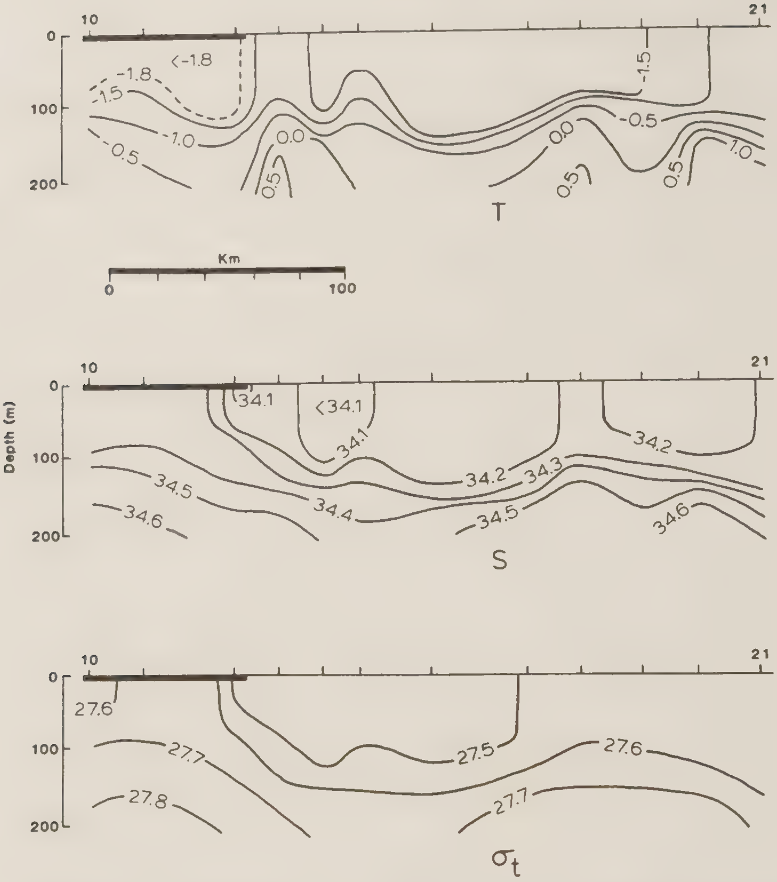

Fig. 9. Distributions of temperature (degrees Celsius), salinity (psu), and density (as σ_t) along 40°W during leg 1, June 16–18, 1988. Data below 200 m were unreliable and are not presented (see text).

on any of the transects (in qualitative agreement with Figure 5). This transect showed clearly, on both crossings, the cold upper layer and the warm CDW core at about 400 m. The warm core was more widespread and had higher temperatures (>2.0°C) in the later than in the earlier transect, and it extended to deeper than the maximum sample depth of 1500 m. The later transect exhibited considerably more complexity than the earlier one.

The literature alludes to a frontal structure, the Scotia Front, which forms the northern boundary of the WSC. *Patterson and Sievers* [1980] arbitrarily chose the 1.5°C isotherm in the CDW to define the Scotia Front. Each of the vertical transects shows a complex region wherein CDW temperatures increased from about 0.5° to 1.5°C. Given the large zonal gaps between our transects, and the regional mesoscale complexity, however, it is not possible to demonstrate continuity of an east-west frontal structure between the transects. The lateral deep temperatures (Figures 4 and 5) suggest that such a structure was present, but the interpretation shown invokes considerable interpolation between the transects. *Foster and Middleton* [1984] were unable to locate the Scotia Front, other than an apparent short segment north of the South Orkney Islands, during summer. They concluded, on the basis of their data from east of about 50°W, that the frontal system had disintegrated into a field of mesoscale eddies which broadened in the zonal sense toward the east.

The interrelations between the upper layer water temperature and the sea ice cover were typical of those observed elsewhere in the marginal ice zones [e.g., *Muench and Schumacher*, 1985]. The ice edge location as observed from the vessel fluctuated widely during the field program in response to local winds. The indicated locations (Figure 1) represent the location that was farthest north as observed from the vessel for each leg. On two occasions (at the northernmost ice edge crossings on August 10–11 and on July 26–28; Figures 7 and 10) the ice edge coincided roughly with the −1.0°C surface isotherm. This is the approximate ambient water temperature above which sea ice melts, and ice which is swept into water warmer than this normally melts within a few days. On other occasions the ice edge was in colder water well south of the −1.0°C isotherm, suggest-

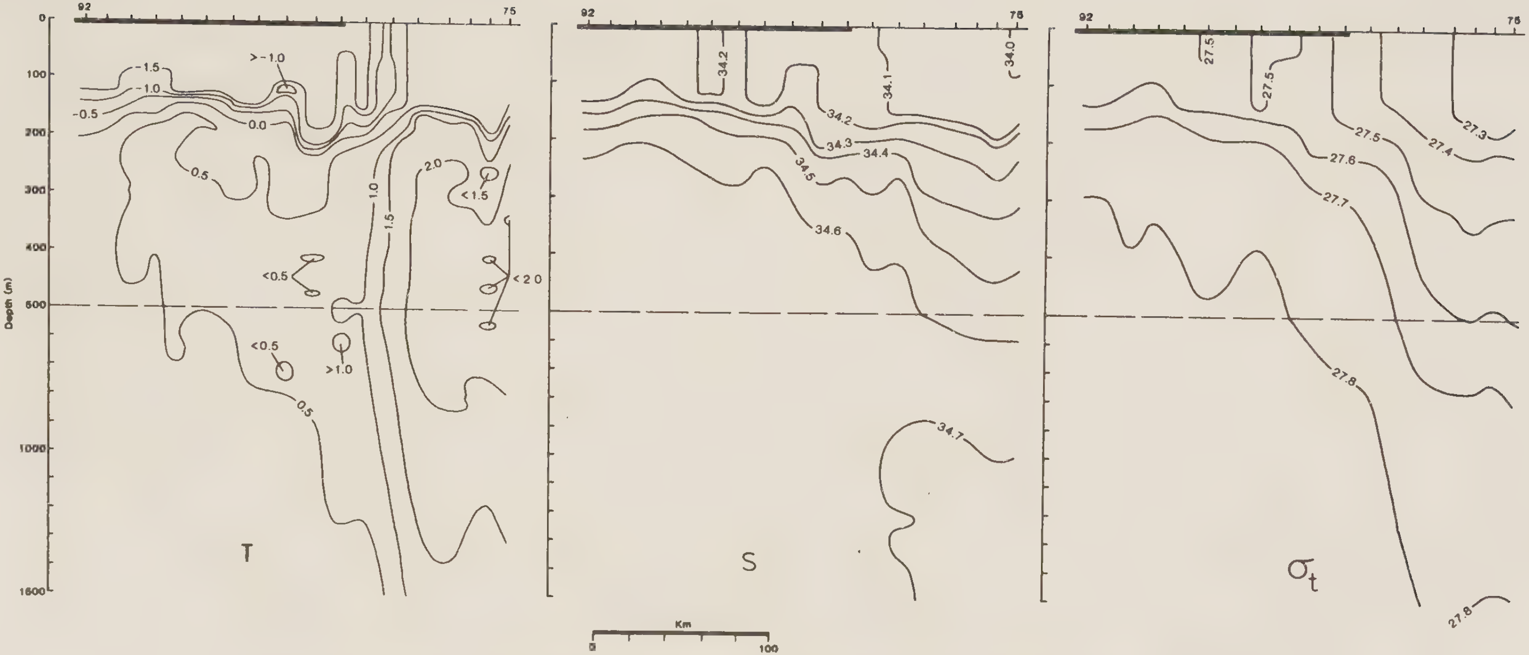

Fig. 10. Distributions of temperature (degrees Celsius), salinity (psu), and density (as σ_t) along 40°W during leg 2, July 26–28, 1988.

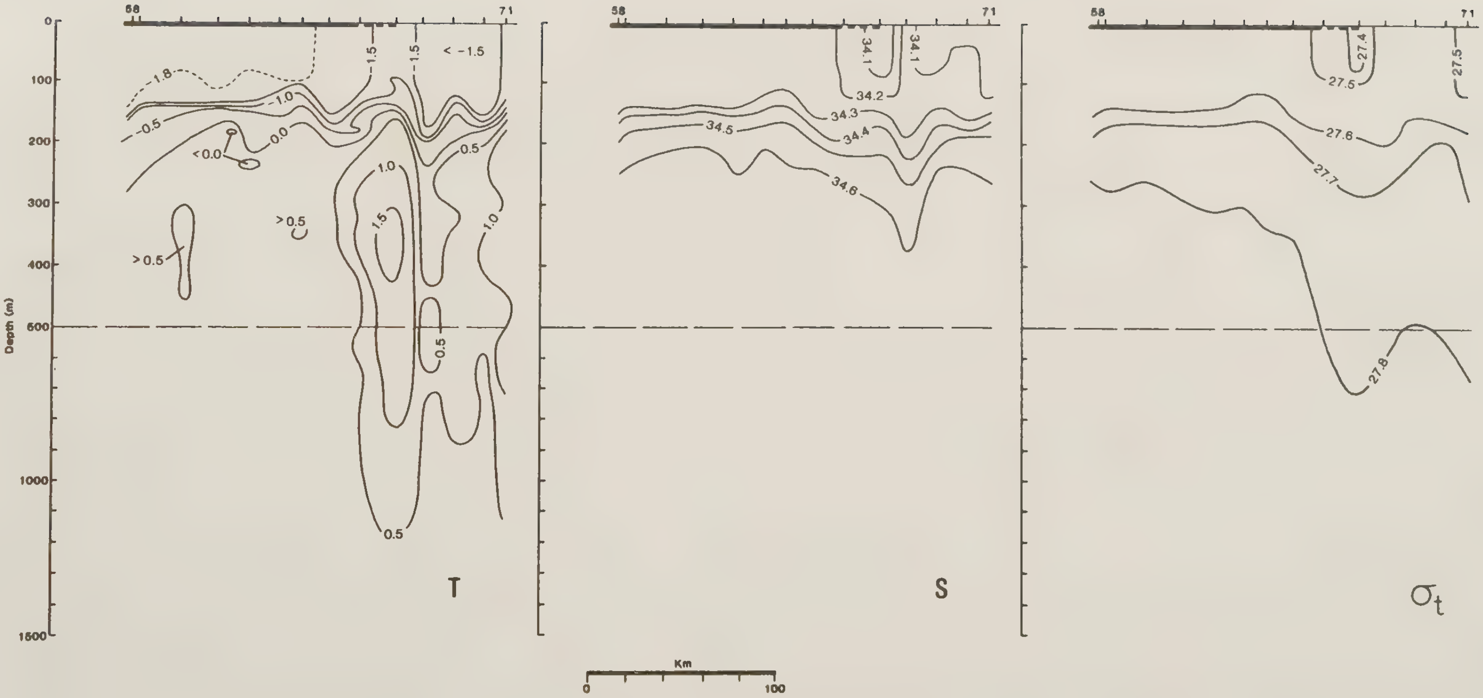

Fig 11. Distributions of temperature (degrees Celsius), salinity (psu), and density (as σ_t) along 35°W during leg 2, July 22–24, 1988.

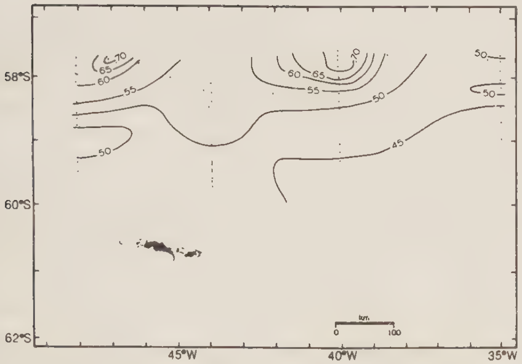

Fig. 12. Dynamic topography of the sea surface relative to the 1500-dbar level during leg 2, July 18 to August 13, 1988. The contour interval is 0.05 dyn m.

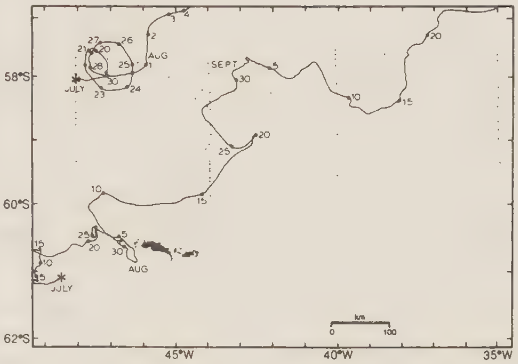

Fig. 13. Drift tracks for the longest record of three obtained from surface-drogued, open water drifters (entrained in the eddy, northwest part of study area) and for an ice-mounted drifter (see text). Circles indicate 1-day intervals for the drogued drifter and 5-day intervals for the ice-mounted drifter. Month and day are given as appropriate at interval points except where space did not permit this. Launch sites for drifters are indicated by asterisks.

ing that the edge had been blown southward from the equilibrium position where input of ice from the south is balanced by melting. Low-salinity lenses due to ice melting at the edge were present on the August 10–11 transect, the June 16–18 transect, and the July 22–24 transect. A low-salinity lens underlaid the ice south of the edge on the July 31 to August 2 transect and may have been the remnant of an earlier ice edge melting event.

3.2. *Circulation*

The baroclinic circulation was derived by constructing dynamic topographies of the sea surface relative to the 500-dbar, 1000-dbar, and 1500-dbar pressure surfaces. Each of these showed the same pattern, with baroclinic current speeds decreasing monotonically with increasing depth so that the surface topography relative to 1500 dbar showed features most clearly (Figure 12). The study region south of the 0.50 dyn m isoline showed little baroclinic flow. The northern part was dominated by a flow which trended slightly north of eastward, as shown by the 0.50 dyn m isoline, and had speeds of order 5–10 cm/s. This flow direction roughly parallels the trends suggested by the horizontal and isopycnal temperature and salinity distributions (Figures 3–5) and is consistent with the regional eastward transport.

The two deep warm patches along 57.5°S (Figures 3–5) were reflected in the baroclinic field as anticyclonic features imbedded within the eastward flow. These extended north beyond the study area and were not completely sampled; however, they appeared to be centered approximately on 40°W and 47°W. They were of order 100 km in horizontal dimension and had associated baroclinic surface current speeds exceeding 40 cm/s for the eastern feature and of nearly 30 cm/s for the western feature. The near-surface-drogued, Argos-tracked drifters which were deployed at the outset of leg 2 provided direct observations of the westernmost of these two features and defined it clearly as an eddy (Figure 13). One of these drifters became entrained within the eddy and executed more than two complete revolutions before exiting it toward the north. This drifted with speeds of 42–54 cm/s from the time it was actually entrained up to its final ejection from the eddy. Movement of the center of the roughly circular trajectory suggests that the eddy was migrating eastward with a speed of about 5 cm/s. Two additional drifters became briefly entrained in the eddy and then exited toward the north after being carried about 90° counterclockwise. Once beyond the influence of the eddy, they drifted toward the north-northeast out of the study region.

Smaller features which resembled eddies were identifiable in the dynamic topography just south of the center of the 48°W transect (an anticyclonic feature suggested by the 0.50 dyn m isoline) and in the northern part of the 35°W transect (an anticyclonic feature suggested by the 0.50 dyn m isolines). The two anticyclonic features had elevated core temperatures (Figures 3 and 4) and may have been warm-core eddies. The widespread occurrence of such eddies is consistent with previously published observations that the eastern Scotia Sea is rich in mesoscale eddies [*Foster and Middleton*, 1984].

Ice floe drift, observed with the single surviving Argos location unit, was as follows (Figure 13). Directly following its launch and prior to August 10 the floe appears to have been trapped in a region of sluggish net flow west of the South Orkney Islands. In late August the floe exited the region and became entrained into the stronger eastward regional currents. The mean drift speed from August 10 to September 15, after the floe had exited the region west of the South Orkneys and while it remained in the study region, was approximately 17 cm/s. Day-to-day drift speeds during this interval varied from about 40 cm/s eastward (August 10–15) to less than 5 cm/s and in a westward direction (August 20–25). A southward deflection of the floe trajectory on September 10–15 at 39°W coincided roughly with the eddy or meanderlike feature which had earlier appeared to be centered on 40°W. Interpretation of the ice floe movement requires caution, since ice drift is influenced by surface winds as well as by currents. Because of icing and hardware problems associated with the shipboard anemometer, no reliable wind observations were available during leg 2. Hence it is not possible to apply a wind correction to the floe drift. We cannot determine in the absence of wind data whether fluctuations in drift speed and direction were responses to circulation features or to local winds.

4. DISCUSSION

One of the potentially significant aspects of the study area lies in the possibility that it is a site for vertical convection and deep ocean ventilation. It was pointed out in the introduction that previous authors working with summer oceanographic data had suggested the WSC to be in part a vertically convective region characterized by reduced stability. Our winter data clearly encompass a region of mixing between Weddell and Scotia Sea waters; however, these data do not reveal deep convection. Only in one instance did the *TS* structure suggest a possible past convective event. In the central part of the final 48°W transect a narrow (less than 20 km, as defined by a single CTD cast), cold (<0°C), saline (0.1 psu more than ambient at the same depth) feature reminiscent of a convective feature was present (Figure 7). This feature was, however, decoupled from the surface by the upper mixed layer and extended down to only about 700-m depths. If it had been in fact a convective feature, it did not appear to be active at the time that the transect was occupied.

Occurrence of deep convection presupposes that stratification is decreased, either as a precurser and/or as a result of the convection. However, stratification, due primarily to salinity, was only slightly less than that measured in summer. Significant weakening of the stratification during winter would require brine enrichment of the upper layers through ice formation. This process would presumably be augmented by the cessation of input of low-salinity ice meltwater from upstream (i.e., the Antarctic Peninsula coastal region and Bransfield Strait). In fact, the regional ice advance appears to occur primarily through wind forcing of the existing ice floes toward the northeast, and the primary site of ice formation and brine rejection lies in the divergent ice field in the Weddell Sea farther south [*Ackley*, 1979, 1984; *Limbert et al.*, 1989]. It is probable that the winter presence of ice in the southern Scotia Sea actually inhibits deep convection by impeding local ice formation and consequent brine rejection. This was also borne out by shipboard ice observations during the 1988 program. Despite a net ice edge advance of as much as 200 km during the field program, the advancing ice was made up primarily of young ice and first-year floes with a few scattered multiyear floes, and little frazil or pancake ice was observed. The "upstream" area in the Weddell Sea is overlain year-round by multiyear pack ice and is not a site for significant new winter ice growth and brine rejection.

The two warm-core cyclonic features along 57.5°S are inherent to the typical regional pattern. There are several possible sources for such mesoscale features in the southern Scotia Sea. *Foster and Middleton* [1984] speculated that similar features observed by them were due either to baroclinic instability or to the development of a plane mixing layer due to turbulent shear flow between the converging water masses farther west. *Klinck* [1985] has documented the eastward passage of rings through Drake Passage at irregular 1.5- to 2-month intervals. Given the observed eastward eddy drift of 5 cm/s, the 400-km spacing between our two observed features would be approximately consistent with the intervals observed by Klinck. *Gordon et al.* [1977] observed a sharp northward bend in the Polar Frontal Zone slightly to the northwest of the observed eddy, and it is possible that segments of the Polar Frontal Zone detach periodically to form eddies which then drift eastward through the Scotia Sea. Vertical temperature inversions from 200 to 400 m in the northern part of the transect, combined with temperatures above 2°C, suggest that these waters were derived from the Polar Frontal Zone [see *Gordon et al.*, 1977]. This origin would be consistent with the apparent presence within the eddy of upper layer temperature inversions which typify Polar Front waters.

Once adrift in the Scotia Sea, the eddies or meanders might behave as planetary waves (see, for example, *LeBlond and Mysak* [1978]). Such waves tend in a beta plane, a reasonable approximation at 60°S, to migrate westward. Westward migration of order 5 cm/s superimposed on an eastward flow of order 10 cm/s would yield the observed eastward migration rate of 5 cm/s. Both a westward migration rate of 5 cm/s and the wavelength (spacing between) of the two observed features are consistent with planetary wave behavior, though a more quantitative analysis is beyond the scope of this paper.

Cyclonic eddies have been hypothesized to precondition water to deep convection by supplying deep water to the sea surface where it can be subjected to cooling and possibly brine enrichment [*Killworth*, 1979]. *Gordon* [1978] detected such a feature in the eastern Weddell Sea. The *MIZEX (Marginal Ice Zone Experiment) '87 Group* [1989] reported seeing deep convective features along the winter Greenland Sea ice edge. These latter features were, however, observed in regions where ice was forming and brine was being rejected into the water column, reducing the static stability interior to the preexisting eddy. The Scotia Sea feature which was identified above by a drogued drifter trajectory as a mesoscale eddy was anticyclonic and did not have reduced stability interior to the eddy. Rather, the upper layer overlying the eddy had increased static stability coincident with lowered salinity. It seems probable that the salinity lowering came about when sea ice, exposed to the higher temperatures overlying the eddy, melted and the meltwater became trapped in the closed eddy circulation. Given that the southern Scotia Sea is a site during winter of net ice melting, rather than of ice formation, this situation would be expected to occur quite commonly. The anticyclonic mesoscale feature farther west, while it did not show a lenslike, low-salinity upper layer, had increased static stability across the main pycnocline at 150–200 m because of increased temperatures and lowered salinities in the upper layer.

Water mass analyses suggest that the water characteristics observed in the southern central Scotia Sea during winter 1988 can be derived from mixing between Weddell Sea and Scotia Sea water types. A family of curves representing the potential temperature-salinity characteristics observed in winter 1988 is presented in Figure 14. Also shown is a potential temperature-salinity envelope derived from data obtained in the northwesternmost Weddell Sea during autumn (March) 1986 as reported by *Husby and Muench* [1988]. These latter data were taken between 48°–53°W and 62°–65°S, an area which we expect is the primary Weddell Sea source region for the WSC. The deepest waters observed in the southern Scotia Sea (1500 m) have θ-S properties identical to Weddell Sea water derived from just above the warm core of the Weddell Warm Water layer. This water type occurs at 300–400 m depth in the Weddell Sea and presumably flows northward into the study region through the gap west of the South Orkney Islands. Warm core water

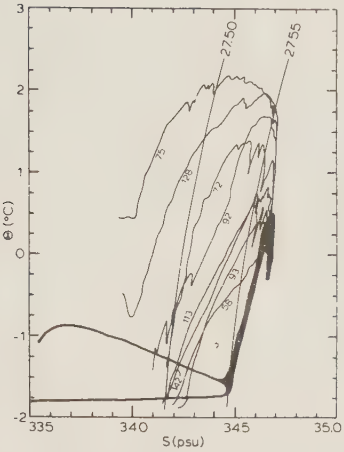

Fig. 14. Potential temperature-salinity curves representing the study region. Numbers adjacent to curves coincide with cast numbers given in Figure 1. The heavy curve is the envelope derived from autumn 1986 data taken in the northwestern Weddell Sea, a source region for the Weddell-Scotia Confluence, by *Husby and Muench* [1988].

from the Weddell Sea is denser than any observed in the southern Scotia Sea, and after entering the Scotia Sea it had probably sunk to its own density level below our 1500-m maximum sampling depth. Water observed in the upper 500–1000 m of the southern Scotia Sea during winter can be derived through isopycnal mixing between the CDW and the Weddell Sea's cold, uppermost layer. The numerous low-temperature layers which were present in the temperature maximum regions are aligned on the θ-S plots along equal potential density curves, consistent with isopycnal interleaving and mixing.

A significant gap exists on the θ-S plot between the southern Scotia Sea and the northwestern Weddell Sea waters, as indicated by a question mark in Figure 14. Presumably, the water types corresponding to this area were situated between our study area and the northwestern Weddell Sea (south of the South Scotia Ridge). The profile from station 58, which we might expect on the basis of the horizontal temperature distributions (Figure 3) to fall close to the Weddell Sea source, trends strongly at middepths toward the northwestern Weddell Sea profiles.

The concept of mixing between upper layer Weddell Sea waters and deeper waters in the Scotia Sea is not a new one. *Deacon and Foster* [1977, Figure 5] prepared a diagram showing lateral mixing paths between the Weddell Sea and the Scotia Sea along about 50°W. Their diagram shows clearly that upper layer Weddell Sea water can be expected to mix laterally with deeper Scotia Sea water. The above water mass analyses demonstrate that such mixing was occurring during winter 1988 and that it was able to account for the observed southern Scotia Sea water characteristics.

Our results do not support previous hypotheses, based upon summer data, which suggest that southern Scotia Sea water is modified through air-sea exchange or continental margin mixing processes, rather than being derived through mixing between Weddell Sea and Scotia Sea waters. In fact, the water type which has been characterized by previous authors as WSC water was not in evidence during winter 1988. We offer three possible explanations. One is that our study region was situated far enough east that WSC water which was presumably formed to the west had been diluted sufficiently through mixing that it was no longer identifiable. A second possibility is that WSC water was present along and south of the axis of the South Scotia Ridge, south of the study region. This seems unlikely, however, since the continual presence of sea ice in that region would have greatly inhibited surface freezing and the resulting convection presumably needed to form WSC water. A final explanation might be simply that there is a large year-to-year variability in the region. This last argument is consistent with the large variation in extent of WSC water which has been reported by the various authors cited above. If in fact the Weddell Sea upper layer water forms a significant proportion of WSC water, as implied by the above discussion, then unusually low upper layer salinities in the Weddell Sea might result in low salinities in the Weddell-Scotia Confluence. Resolution of these questions awaits the acquisition of midwinter data from a broader area, including regions to the west and south.

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REFERENCES

Ackley, S. F., Mass-balance aspects of Weddell Sea pack ice, *J. Glaciol.*, *24*, 391–405, 1979.

Ackley, S. F., Sea ice data buoys in the Weddell Sea, *Rep. 84-11*, Cold Reg. Res. and Eng. Lab., Hanover, N. H., 1984.

Comiso, J. C., and H. J. Zwally, Polar microwave brightness temperatures from Nimbus-7 SMMR: Time series of daily and monthly maps from 1978 to 1987, *NASA Ref. Publ. 1223*, 82 pp., 1989.

Deacon, G. E. R., and T. D. Foster, The boundary region between the Weddell Sea and Drake Passage currents, *Deep Sea Res.*, *24*, 505–510, 1977.

Deacon, G. E. R., and J. A. Moorey, The boundary region between currents from the Weddell Sea and Drake Passage, *Deep Sea Res.*, *22*, 265–268, 1975.

Foster, T. D., and J. H. Middleton, The oceanographic structure of the eastern Scotia Sea, I, Physical oceanography, *Deep Sea Res.*, *31*, 529–550, 1984.

Gordon, A. L., Deep Antarctic convection west of Maud Rise, *J. Phys. Oceanogr.*, *8*, 600–612, 1978.

Gordon, A. L., Spatial and temporal variability within the southern ocean, in *Antarctic Ocean and Resources Variability*, edited by D. Sahrhage, pp. 41–56, Springer-Verlag, New York, 1988.

Gordon, A. L., D. T. Georgi, and H. W. Taylor, Antarctic Polar Front Zone in the western Scotia Sea—Summer 1975, *J. Phys. Oceanogr.*, *7*, 309–328, 1977.

Husby, D. M., and R. D. Muench, Hydrographic observations in the northwestern Weddell Sea marginal ice zone during March 1966, *Tech. Memo. NOAA-TM-NMFS-SWFC-106*, Natl. Mar. Fish. Serv., Southwest Fish. Cent., Natl. Oceanic and Atmos. Admin., Monterey, Calif., 1988.

Killworth, P. D., On "chimney" formations in the ocean, *J. Phys. Oceanogr.*, *9*, 531–554, 1979.

Klinck, J. M., EOF analysis of central Drake Passage currents from DRAKE 79, *J. Phys. Oceanogr.*, *15*, 288–298, 1985.

LeBlond, P. H., and L. A. Mysak, *Waves in the Ocean*, Elsevier, New York, 1978.

Limbert, D. W. S., S. J. Morrison, C. B. Sear, P. Wadhams, and M. A. Rowe, Pack-ice motion in the Weddell Sea in relation to weather systems and determination of a Weddell Sea sea-ice budget, *Ann. Glaciol.*, *12*, 104–112, 1989.

Marginal Ice Zone Experiment (MIZEX) '87 Group, MIZEX east 1987—Winter marginal ice zone program in the Fram Strait and Greenland Sea, *Eos Trans. AGU*, *70*, 545–555, 1989.

Muench, R. D., and J. D. Schumacher, On the Bering Sea ice edge front, *J. Geophys. Res.*, *90*, 3185–3197, 1985.

Nelson, D. M., W. O. Smith, Jr., L. I. Gordon, and B. A. Huber, Spring distributions of density, nutrients and phytoplankton biomass in the ice edge zone of the Weddell-Scotia Sea, *J. Geophys. Res.*, *92*, 7181–7190, 1987.

Nelson, D. M., W. O. Smith, Jr., R. D. Muench, L. I. Gordon, C. W. Sullivan, and D. M. Husby, Particulate matter and nutrient distributions in the ice-edge zone of the Weddell Sea: Relationship to hydrography during late summer, *Deep Sea Res.*, *36*, 191–209, 1989.

Patterson, S. L., and H. A. Sievers, The Weddell-Scotia Confluence, *J. Phys. Oceanogr.*, *10*, 1584–1610, 1980.

Zwally, H. J., J. C. Comiso, C. L. Parkinson, W. J. Campbell, F. D. Carsey, and P. Gloersen, Antarctic sea ice, 1973–1976: Satellite passive-microwave observations, *NASA Spec. Publ. SP-459*, 1983.

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DEVELOPMENT OF LARVAE AND JUVENILES OF THE ALFONSINS, *BERYX SPLENDENS* AND *B. DECADACTYLUS* (BERYCIDAE, BERYCIFORMES)

Bruce C. Mundy

ABSTRACT

The larval development of the alfonsins, *Beryx* spp., is described from specimens collected from the central North Pacific Ocean (29°N, 179°E) during July 1984, primarily in the upper 50 m. Yolk-sac larvae, 1.5–3.0 mm standard length (SL), have pigment at the forebrain and midbrain, the anterior end of the oil globule, over the intestine above the anus, and around the tip of the notochord. Pelvic buds form at 1.5–3.0 mm SL; flexion occurs between 3.7 and 6.0 mm SL. Fin ray formation is complete and scales are formed by 15 mm SL. Characters useful for identifying *Beryx* larvae include very elongate, early forming pelvic rays and anterior dorsal spines; a slightly S-shaped intestine about half the standard length; and sparse pigment restricted to internal pigment at the gas bladder, over the posterior intestine, and a spot located asymmetrically on the forebrain. Spines on the first lower infraorbital, characteristic of adult *Beryx*, develop at 3.8–4.5 mm SL. Juvenile *B. splendens* and *B. decadactylus*, from the North Atlantic, differ from each other in dorsal fin ray count.

The alfonsins (Berycidae) are moderately large, usually bright red fishes found in tropical and temperate shelf or slope waters of all oceans (Busakhin, 1982). The family contains two genera, *Beryx* and *Centroberyx*, which are easily distinguished by meristics and head spination (Zehren, 1979). *Beryx* contains two species: *B. decadactylus* from the Atlantic, Mediterranean, southern Indian Ocean, western Pacific rim, and Hawaii in the central Pacific plate; and *B. splendens* from all temperate and tropical areas except the Mediterranean Sea and the eastern Pacific Ocean north of the Equator (Busakhin, 1982). *Beryx mollis* is a synonym of *B. splendens* (Heemstra, 1986). Commercial fisheries for alfonsin exist where they are abundant (Woods and Sonoda, 1973), particularly in the central and western Pacific (Uchida and Tagami, 1984; Seki and Tagami, 1986). Although both species of *Beryx* are abundant and commercially important, relatively little is known of their early life history (Keene and Tighe, 1984). Onishi (1966; 1968) described the eggs, yolk-sac larvae, and preflexion larvae, and Okiyama (1988) described a single 10.0 mm larva of *B. splendens*. Juvenile *Beryx* have been described, first as a separate genus, *Actinoberyx* (Roule, 1924), and more recently under both generic names (Fourmanoir, 1976; Krefft, 1976) as reviewed by Busakhin (1982).

This paper presents the first complete ontogenetic description of *Beryx* species. Large larvae and small juveniles of *B. splendens* are compared to those of *B. decadactylus*, and developmental features of *Beryx* pertinent to future phylogenetic studies of the Beryciformes are reviewed.

MATERIALS AND METHODS

Larvae were collected at the Southeast Hancock Seamount (29°48′N, 179°04′E) during 9–28 July 1984. Stepped, oblique plankton tows were taken over the seamount and at areas approximately 20 km to the west during day and night. A three-net Tucker trawl (1 m^2 effective mouth opening and 0.333 mm bar mesh), containing calibrated flowmeters, was towed at 2–3 kn for 14–38 min per net. Samples were taken at depth strata of 0–25, 25–50, 50–100, and 100–200 m, with additional oblique tows taken at 0–50 and 0–100 m as the trawl was retrieved from the deeper strata. Samples were fixed in 10% buffered formalin. In the laboratory, samples were processed by the methods of Smith and

Richardson (1977). *Beryx* larvae (133 specimens) were removed from sorted lots of fish larvae and preserved in 70% ethanol (Lavenberg et al., 1984) approximately 18 months after collection. Additional specimens of large larvae and small juveniles of *B. splendens* and *B. decadactylus* from the Atlantic Ocean were borrowed from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology, Harvard University (MCZ); the U.S. National Museum of Natural History (USNM), and the Atlantic Reference Center, Huntsman Marine Laboratory (ARC).

Yolk-sac larvae of *B. splendens* were obtained by artificial fertilization using gametes from identified adults caught by handline at the Hancock Seamount on 30 July 1984. The eggs and larvae were held in seawater at 23°–25°C. The eggs hatched after 27.5 h, and larvae, which were not fed, were preserved in 5% buffered formalin 60 h after hatching.[1]

The developmental series from the plankton samples was established using the serial technique of Moser and Ahlstrom (1970). Terminology of developmental stages follows Ahlstrom et al. (1976). That of head spination follows Johnson and Washington (1987), except the lacrimal is referred to here as the first infraorbital, the small spines that form secondarily on larger spines are called accessory spines, and the spines of the preopercle are distinguished as being on anterior and posterior ridges. In this paper, SL refers to standard length in flexion and postflexion specimens, and to notochord length in preflexion larvae. Measurements were taken with an ocular micrometer in a dissection microscope as defined by Moser and Ahlstrom (1970) and Leis and Rennis (1983). Illustrations were made using a camera lucida. Specimens were stained lightly with alizarin red S to enhance visibility of head spines and fin elements.

DESCRIPTION

Distinguishing Features.—Yolk-sac *Beryx* from plankton samples were initially identified by reference to the reared specimens (Fig. 1A). The combination of characters that allows identification of preflexion larvae from plankton samples includes 23 myomeres, an uncoiled intestine, a preanal length approximately 50% SL, early forming pelvic fin buds indicating early development of the pelvics, and an unusual pigment pattern consisting of melanophores restricted to the forebrain and midbrain, the anterior edge of the oil globule, the end of the intestine, and around the notochord tip. Larger *Beryx* larvae are characterized by very long, early forming pelvic rays and anterior dorsal elements, a slightly curved intestine, a preanal length 45–56% SL (Table 1), and sparse pigment (restricted to internal pigment located asymmetrically over the forebrain, pigment on the cranium in postflexion larvae, internal pigment at the gas bladder and over the posterior intestine, and external pigment at the anus) (Figs. 1–3).

Larvae with elongate dorsal and pelvic fins which superficially resemble *Beryx* in preflexion and flexion stages are described by Leis and Rennis (1983), Ahlstrom et al. (1984), Keene and Tighe (1984), Olney (1984), Okiyama (1988), and Leis and Trnski (in press). *Beryx* larvae show the greatest similarity to melamphaid larvae, particularly *Melamphaes.* Both genera are very similar in body shape, intestine shape and length, and in the sequence of fin formation (Keene and Tighe, 1984). Melamphaids differ from berycids in pigment pattern, meristics, and head spination (Ebeling, 1962; Ebeling and Weed, 1963; 1973; Keene and Tighe, 1984).

Postflexion *Beryx* larvae and juveniles have 10+9 principal caudal rays, characteristic of the Beryciformes in the Percomorpha, and develop the unpaired, procurrent caudal fin spines of the Beryciformes (Lauder and Liem, 1983). Postflexion *Beryx decadactylus* larvae have 16–18 dorsal rays versus 13–15 in *B. splendens* (Woods and Sonoda, 1973). No other character identifies larvae of the two species, although the presence of internal branchial pigment in *B. decadactylus* may prove useful in identifying postflexion larvae (see comparison of the two species later in this paper). Identification of small *B. decadactylus* is not possible at this time. Larvae of the confamilial *Centroberyx* are undescribed and are ex-

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[1] Y. Lamadrid-Rose, Hawaii State Division of Aquatic Resources, Honolulu, Hawaii 96813 (pers. comm., April 1986).

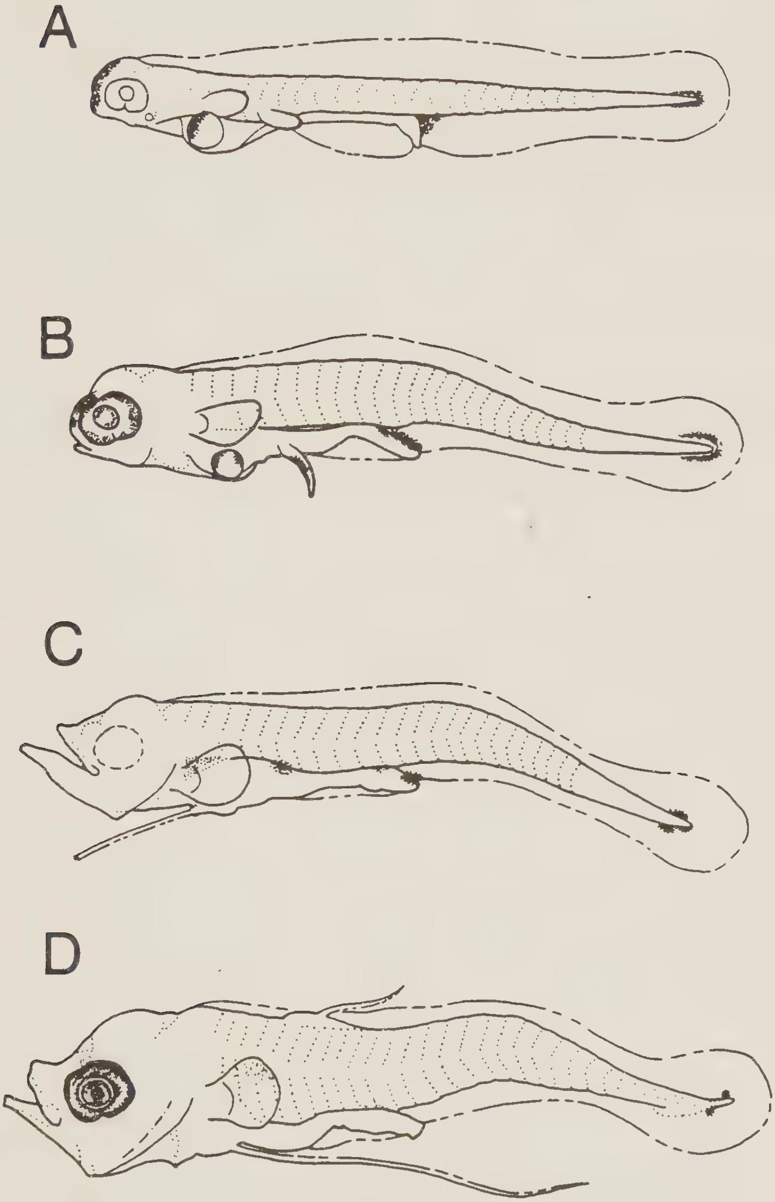

Figure 1. Preflexion larvae of *Beryx* spp. All except A were collected at Southeast Hancock Seamount. (A) reared larva of *B. splendens*, 3.0 mm SL. (B) 2.1 mm SL. (C) 3.0 mm SL. (D) 3.3 mm SL.

pected to be very similar to *Beryx*. Postflexion *Centroberyx* will have fewer anal rays (IV, 12–16) than *Beryx* (III–IV, 25–32) (Busakhin, 1982). Postflexion *Beryx* larvae from the Hancock Seamount with 14–15 dorsal soft rays and all fin rays formed (Fig. 3) were identified as *B. splendens*. North Atlantic specimens with 17–18 dorsal rays were identified as *B. decadactylus*. With the exception of the reared and largest specimens, the material described from the Hancock Seamount

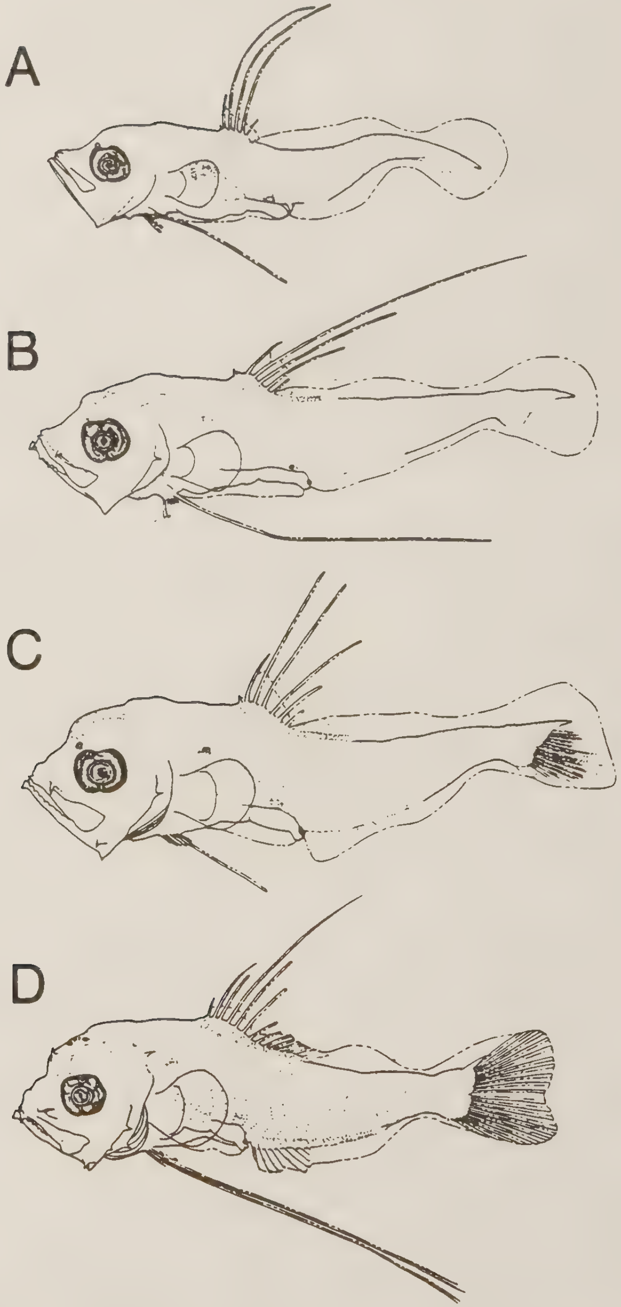

Figure 2. Flexion larvae of *Beryx* spp. collected at the Southeast Hancock Seamount. (A) 4.0 mm SL. (B) 4.6 mm SL. (C) 5.0 mm. SL. (D) 5.2 mm SL.

could include *B. decadactylus* as well as *B. splendens.* No differences were found among the larvae to indicate that more than one species was present in collections from the Hancock Seamount.

Morphology (Tables 1, 2). — Recently hatched larvae (Fig. 1A) have a large oil globule (mean diameter = 0.15 mm, 0.03 SD, N = 6) at the anterior end of the ovoid yolk, unpigmented eyes, and an unformed mouth. The yolk measures 0.34 mm in mean length (0.13 SD) and 0.15 mm in mean depth (0.03 SD). The intestine is straight until the downward bend before the anus. Pelvic and pectoral buds form before the yolk is absorbed. The mouth forms, the eyes become pigmented, and the pelvic buds begin to elongate as the yolk and oil globule disappear (Fig. 1B). After the yolk is absorbed, the body deepens, the snout becomes pointed, and the head assumes a characteristically concave dorsal profile (Figs. 1C–D, 2A–B); this profile may be due to tissue shrinkage caused by preservation. The intestine becomes slightly curved and develops a distinct midgut and hindgut. Late preflexion larvae become laterally compressed, remaining so through transformation.

During flexion, the body deepens and the gut becomes more differentiated (Fig. 2B–D). The profile of the head remains concave with a pointed snout, which becomes rounded near the end of flexion. In flexion and postflexion larvae, the body depth, head depth, and head length increase relative to the SL, and a prominent gas bladder is present (Figs. 2, 3). In postflexion *Beryx* larvae the dorsal profile of the head becomes strongly convex (Fig. 3). Preanal length shortens with development, from 56 to 45% SL, but lengthens to 53% SL in juveniles (Table 1; Fig. 4), the midgut and hindgut become more distinct, and the midgut becomes coiled.

A preanal finfold is present. The preanal and remnant dorsal finfolds, midway between the dorsal and caudal fins, are the last parts of the finfold to persist before transformation (Fig. 3B). The remnant dorsal finfold, seen on all postflexion larval specimens, is curiously like the precursor of the adipose fin seen in myctophids (Moser and Ahlstrom, 1970) and percopsids (Auer, 1982). The finfolds are gone at 9.2 mm SL.

Head Spines (Table 3; Fig. 5). — Head spines begin to develop at flexion (Fig. 2A, B). All head spines of *Beryx* are bilateral. The first to appear are spines at the anterior end of the maxilla and at the retroarticular, at 2.8–4.3 mm SL. The large spine on the first infraorbital, characteristic of *Beryx* (Zehren, 1979), develops in midflexion at 3.8–4.5 mm SL, when spines appear along the anterolateral ridge of the preopercle (Fig. 2B). Teeth form on the premaxilla in early flexion and remain prominent through larval development. The frontals develop a rugose texture, and a spine appears posteriorly on the anguloarticular, above the retroarticular, at 3.3–5.0 mm SL (Fig. 2B, C). During late flexion (5.0–6.0 mm SL), other spines appear on the preopercle, interopercle, and posttemporal (Fig. 2D). An unspined supraorbital ridge and a prominent anteromedial spine, both on the frontal, develop at sizes greater than 5.0 mm SL. In postflexion specimens (>7.0 mm SL; Fig. 3B), all spines previously seen are present, and additional spines appear at the tip and along the lateral edge of the dentary. More spines are present on the preopercle and interopercle, including a row of spines on the posterior margin of the preopercle. A small spine is present anterior to the large, first infraorbital spine, and there is a spine on the posterior margin of the dorsal part of the opercle.

In juveniles (≥15 mm SL), additional spines appear at the retroarticular, near the anteromedial frontal spine, on the infraorbitals, and along the supraorbital ridge (Figs. 4A, 5). Several small spines form on the posttemporal, but there are

Table 1. Mean body proportions (mm divided by SL) of larval and juvenile *Beryx* spp., except for classes with only single specimens. N = numbers of specimens. Developmental stages for each size class are 1 = yolk sac, 2 = preflexion, no yolk sac, 3 = flexion, 4 = postflexion, 5 = juvenile

SL	N	Stages	Preanal length	Predorsal length	Prepelvic length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin ray length	Pelvic fin ray length	Dorsal fin ray length
Beryx spp.													
1.0–1.9	12	1	0.54	—	0.30	0.16	0.13	0.03	0.10	0.18	0.06	0.08	—
2.0–2.9	8	1	0.55	0.41	0.26	0.25	0.14	0.06	0.11	0.18	0.07	0.29	0.09
3.0–3.9	25	1–2	0.56	0.40	0.27	0.32	0.14	0.09	0.10	0.22	0.08	0.48	0.34
4.0–4.9	72	2–3	0.54	0.39	0.26	0.32	0.14	0.09	0.10	0.22	0.08	0.39	0.36
5.0–5.9	4	2–4	0.49	0.39	0.28	0.33	0.14	0.09	0.09	0.27	0.09	0.38	0.39
Beryx splendens													
7.0–7.9	4	4	0.45	0.36	0.29	0.29	0.12	0.09	0.09	0.35	0.15	0.76	0.56
9.0–9.9	3	4	0.49	0.38	0.36	0.29	0.17	0.08	0.08	0.38	0.18	0.62	0.25
10.32	1	5	0.45	0.42	0.34	0.30	0.16	0.08	0.09	0.37	0.22	0.83	0.30
15.00	1	5	0.46	0.40	0.34	0.25	0.16	0.07	0.10	0.41	0.22	0.94	2.07
21.72	1	5	0.50	0.43	0.34	0.28	0.18	0.07	0.09	0.40	0.21	0.25	0.32
27.48	1	5	0.53	0.46	0.40	0.27	0.19	0.07	0.10	0.41	0.26	0.75	0.22
Beryx decadactylus													
8.52	1	4	0.46	0.44	0.42	0.32	0.12	0.11	0.08	0.37	0.14	0.63	0.37
10.08	1	5	0.45	0.42	0.34	0.29	0.18	0.09	0.08	0.40	0.21	1.20	0.31
11.52	1	5	0.48	0.33	0.39	0.26	0.17	0.08	0.07	0.38	0.30	1.16	1.20
16.38	1	5	0.53	0.41	0.40	0.26	0.19	0.08	0.10	0.44	0.23	0.93	1.88
21.38	1	5	0.51	0.45	0.42	0.27	0.15	0.09	0.08	0.47	0.23	1.46	1.69
23.28	1	5	0.58	0.44	0.48	0.31	0.18	0.10	0.08	0.46	0.24	2.19	2.26

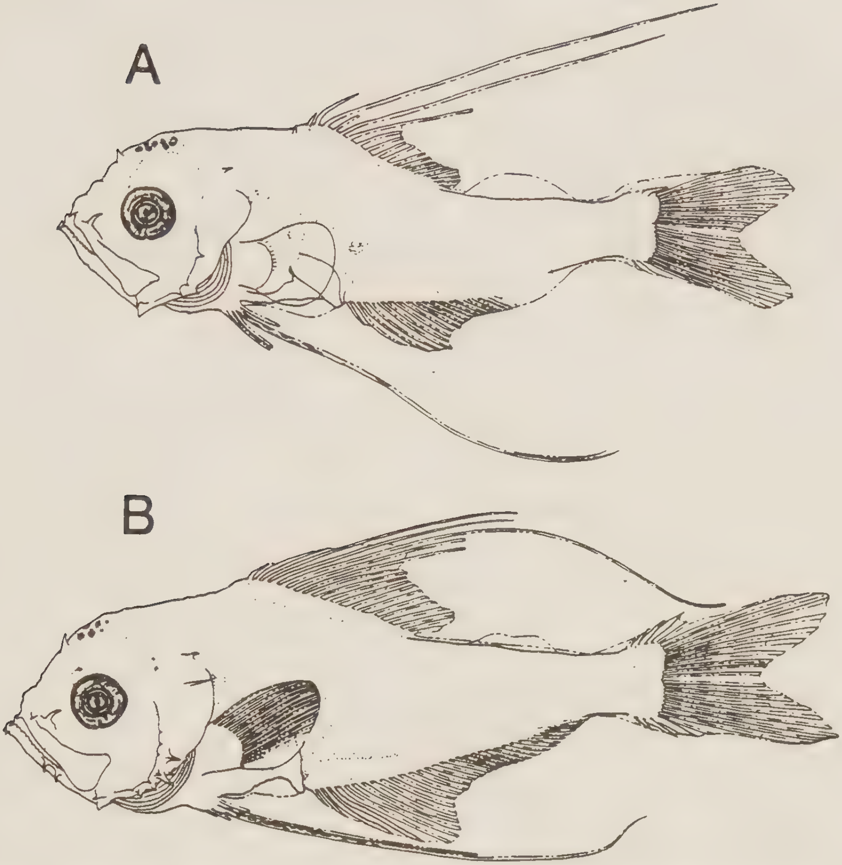

Figure 3. Postflexion larvae of *Beryx splendens* collected at the Southeast Hancock Seamount. (A) 6.0 mm SL. (B) 7.5 mm SL.

no spines on the cleithrum or other pectoral bones. A second opercular spine forms ventral to the first. As many as 13 spines appear on the posterior margin of the interopercle (Table 3). Small accessory spines appear along the upper opercular spine, and on the largest spines near the angles of both preopercular series. In the bones of the jaws, the dentary bears two ridges of spines with a series of large pores between them. The upper jaw bears two spiny ridges on the posterior supramaxilla. Maxillary and retroarticular spines are absent on the largest juvenile (Table 3). The rugose area of the frontal in juveniles bears three serrate ridges. Juveniles also develop a serrate ridge incorporating the anteromedial frontal spine. The bony supraorbital ridge develops small spines. *Beryx* larvae and juveniles lack spines on the parietals and supraoccipital.

With the exception of the spines on the first infraorbital and upper opercle, the larval spines are incorporated into serrate ridges or crests in adult *Beryx* (Woods and Sonoda, 1973; Busakhin, 1982). See Zehren (1979) for a detailed description of adult osteology.

Meristics/Fin Formation (Table 4).—All specimens have 23 myomeres, not including the urostylar segment and the muscle segment anterior to the first myo-

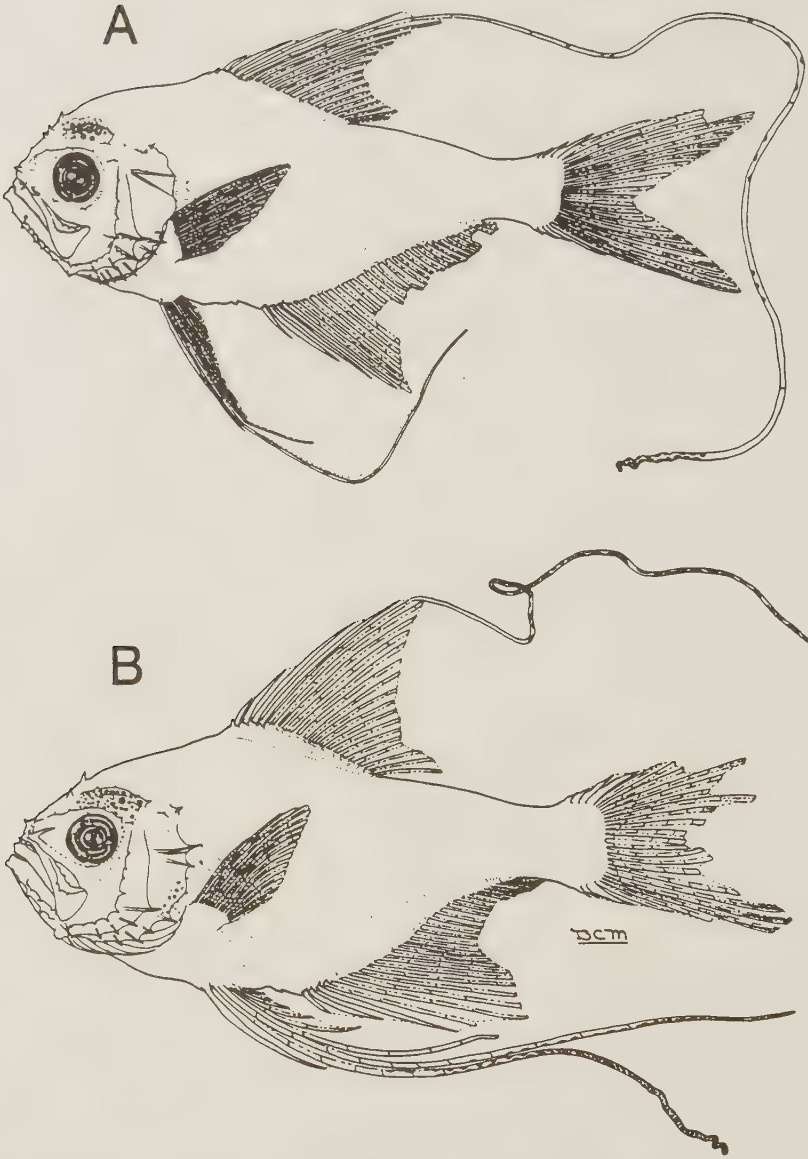

Figure 4. Pelagic juveniles of *Beryx* spp. collected in the North Atlantic. (A) *B. splendens*, 15.0 mm SL (MCZ 068672). (B) *B. decadactylus*, 16.4 mm SL (MCZ 064863). Scales are completely formed on these specimens but are not shown.

septum. Onishi's (1966) count of 30 is clearly an error; the myomere count of teleosts, including the urostylar and anterior segments, is one more than the vertebral count (Fuiman, 1982), which, in *Beryx*, is 24 (Starks, 1904; Woods and Sonoda, 1973; Zehren, 1979). As the intestine shortens, the precaudal myomere number decreases from 11 to 9.

In contrast to most other fishes, the pelvic fin rays are the first to ossify in

Table 2. Measurements (mm) of larval and juvenile *Beryx* spp. Means and standard deviations are given for measurements within each size class, except for classes with single specimens. (See Table 1 for sample sizes and developmental stages for each size class)

SL	Preanal length x̄ (SD)	Predorsal length x̄ (SD)	Prepelvic length x̄ (SD)	Head length x̄ (SD)	Head width x̄ (SD)	Snout length x̄ (SD)	Eye diameter x̄ (SD)	Body depth x̄ (SD)	Pectoral fin ray length x̄ (SD)	Pelvic fin ray length x̄ (SD)	Dorsal fin ray length x̄ (SD)
Beryx spp.											
1.0–1.9	0.91 (0.10)	— (—)	0.50 (0.04)	0.27 (0.06)	0.22 (0.04)	0.05 (0.03)	0.16 (0.02)	0.30 (0.06)	0.09 (0.03)	0.13 (0.04)	— (—)
2.0–2.9	1.37 (0.28)	1.18 (0.09)	0.66 (0.15)	0.64 (0.19)	0.34 (0.09)	0.17 (0.06)	0.27 (0.07)	0.47 (0.15)	0.18 (0.07)	0.79 (0.54)	0.27 (0.10)
3.0–3.9	2.06 (0.21)	1.47 (0.16)	0.98 (0.15)	1.19 (0.18)	0.52 (0.07)	0.35 (0.09)	0.37 (0.04)	0.80 (0.13)	0.30 (0.06)	1.75 (0.53)	1.29 (0.70)
4.0–4.9	2.34 (0.11)	1.68 (0.09)	1.14 (0.09)	1.41 (0.10)	0.60 (0.04)	0.41 (0.04)	0.41 (0.03)	0.97 (0.09)	0.33 (0.07)	1.69 (0.79)	1.58 (0.67)
5.0–5.9	2.63 (0.15)	2.08 (0.14)	1.48 (0.20)	1.74 (0.14)	0.76 (0.08)	0.50 (0.05)	0.49 (0.05)	1.43 (0.18)	0.47 (0.05)	2.05 (1.13)	2.14 (1.14)
Beryx splendens											
7.0–7.9	3.32 (0.07)	2.66 (0.14)	2.17 (0.03)	2.15 (0.08)	0.86 (0.12)	0.63 (0.02)	0.64 (0.04)	2.55 (0.28)	1.11 (0.13)	5.62 (0.51)	4.19 (1.05)
9.0–9.9	4.66 (0.66)	3.64 (0.11)	3.46 (0.73)	2.72 (0.20)	1.56 (0.10)	0.82 (0.08)	0.80 (0.11)	3.56 (0.43)	1.73 (0.13)	5.94 (2.32)	2.34 (0.85)
10.32	4.68	4.38	3.48	3.12	1.62	0.87	0.90	3.84	2.28	8.52	3.06
15.00	6.96	6.00	5.16	3.72	2.40	1.08	1.44	6.12	3.36	14.04	31.08
21.72	10.92	9.36	7.44	6.12	3.96	1.62	1.98	8.64	4.92	5.34	6.96
27.58	14.64	12.66	11.04	7.44	5.28	1.92	2.70	11.40	7.08	20.64	6.12
Beryx decadactylus											
8.52	3.96	3.72	3.60	2.70	1.03	0.96	0.66	3.12	1.22	5.40	3.12
10.08	4.50	4.20	3.42	2.94	1.80	0.90	0.84	4.08	2.10	12.12	3.12
11.52	5.52	3.84	4.44	3.00	1.92	0.91	0.86	4.32	3.48	1.38	13.32
16.38	8.64	6.72	6.60	4.32	3.12	1.32	1.56	7.20	3.72	15.31	30.84
21.00	10.68	9.36	8.76	5.76	3.24	1.80	1.68	9.84	4.92	30.60	35.52
23.28	13.44	10.20	11.28	7.32	4.20	2.28	2.16	10.80	5.64	51.00	52.56

Table 3. Development of head spines in *Beryx* spp. Minimum-modal-maximum numbers of spines are given when a range of spine numbers was found within a size class; + = presence, – = absence. Only minimum and maximum numbers are given when no modal number was found. (See Table 1 for sample sizes and developmental stages for each size class)

SL (mm)	Maxilla	Retro-articular	First infra-orbital	Anterior preopercle	Rugose frontal	Angulo-articular	Interopercle	Frontal	Post-temporal	Supraorbital ridge	Dentary	Opercle	Posterior pre-opercle	Nasal
Beryx spp.														
1.0–1.9		-	-			–	–	–	-	-				
2.0–2.9	-	0-0-1					–	–	–	–	-	–		
3.0–3.9	0-1-1	0-1-1	0-0-1	0-0-1	or +	0-0-1		-			–		-	-
4.0–4.9	1	0-1-1	0-1-1	0-0-2	or +	0-0-1	–	–	–	– or +	–	–	–	–
5.0–5.9	1	1	1	1-3-3	+	1	0-1	0-1-1	0-1-1	– or +	–	– or +	–	–
Beryx splendens														
7.0–7.9	1	1	2	5-5-7	+	1	2-5-5	1	1	+	2-2-3	1	3-4	
9.0–9.9	1	1	1-2-2	4-4-6	+	1	3-5	1	1-1-2	+	2-3-3	1-1-2	2-3-3	–
10.32	1	1	2	2	+	1	4	1	1	+	4	1	3	–
15.00	1	2	2	8	+	1	10	3	1	+	8	2	4	1
21.72	2	1	2	6	+	2	8	6	1	6	22	2	7	1
27.48	–	–	2	8	+	1	13	5	2	11	20	2	8	2
Beryx decadactylus														
8.52	1	1	2	5	?	1	3	1	1	+	3	+	4	–
10.08	1	1	2	5	+	1	5	1	2	1	3	1	4	1
11.52	1	1	2	3	+	1	3	2	2	+	3	1	2	
16.38	1	1	2	7	+	1	4	2	2	2	9	2	5	1
21.00	1	1	2	9	+	1	5	3	2	4	9	3	5	1
23.28	-		2	11	+	1	7	2	2	5	10	1	6	1

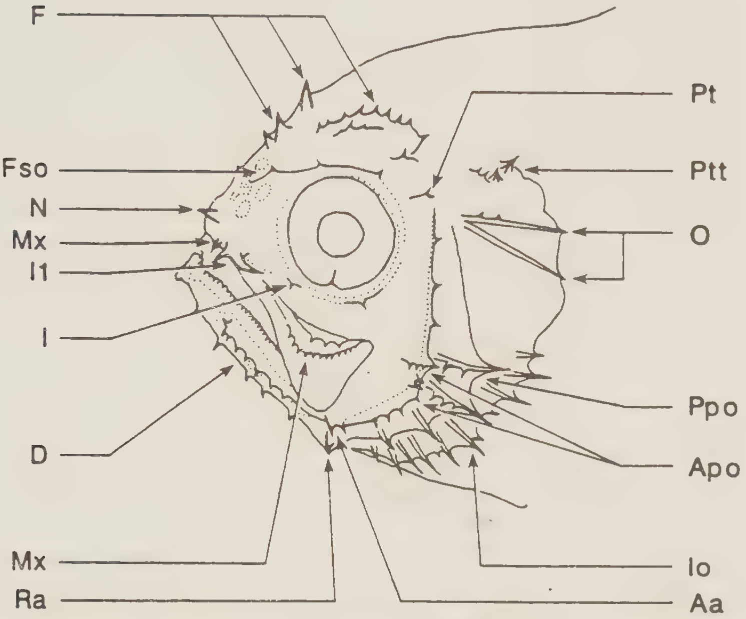

Figure 5. Head spines of *B. decadactylus*, 16.4 mm SL (MCZ 064863). (Aa) anguloarticular; (Apo) anterior preopercle; (D) dentary; (F) frontal; (Fso) supraorbital ridge of frontal; (I) infraorbital; (I1) first infraorbital; (Io) interopercle; (Mx) maxilla; (N) nasal; (O) opercle; (Ppo) posterior preopercle; (Pt) pterotic; (Ptt) posttemporal; and (Ra) retroarticular.

Beryx, at 1.5–3.0 mm SL (Fig. 1B, C). The full adult complement of I, 10–12 pelvic elements (Woods and Sonoda, 1973; Zehren, 1979) is not seen in larvae. Juveniles (≥15 mm SL) have all pelvic elements developed. Pelvic rays are almost invariably broken and difficult to see in the larvae. Only a few specimens have even one or two pelvic rays intact. The greatest pelvic ray length of any of the *Beryx* specimens is over twice the SL (Tables 1, 2); even this ray may have been damaged.

Dorsal fin elements also begin to develop early, at about 2.8 mm SL (Fig. 1D). As with the pelvic rays, the anterior dorsal spines and soft rays are elongate and rarely intact. The pigmented swelling at the distal end of the first dorsal ray of the largest specimens (Fig. 4) suggests that the rays may be longer and more highly ornamented than seen in these specimens, a condition similar to that seen in larval carapids (Govoni et al., 1984) and some larval serranids (Kendall et al., 1984). The greatest dorsal ray length is over twice the SL (Tables 1, 2). Fin element formation proceeds posteriad from the first spine, and the fourth element forms initially as a soft ray, becoming a spine by 6.0 mm SL. The adult complement of IV, 14–15 is formed at sizes greater than 5.9 mm SL (Fig. 3A, B).

Other fin elements form after the dorsal and pelvic elements first appear. Flexion, with formation of the principal caudal rays, begins at about 3.7–4.0 mm SL, and is complete by about 6.0 mm SL when the full complement of 10+9 principal rays is present (Figs. 2D, 3). The four large procurrent spines and single, unsegmented procurrent ray on each caudal lobe are present in specimens larger than 7.0 mm SL (Fig. 3B). The anal fin develops with the caudal, from 4.0 to 7.0 mm SL (Figs. 2, 3). As with the dorsal fin, anal fin element formation proceeds posteriad from the first spine, and the fourth element develops as a soft ray, becoming a

Table 4. Development of fin elements and branchiostegals in *Beryx* spp. Minimum-modal-maximum numbers of elements are given when a range of element number was found within a size class; ? = structures not entirely visible. Only minimum and maximum numbers are given when no modal number was found. (See Table 1 for sample sizes and developmental stages within each size class)

SL (mm)	Dorsal spines	Dorsal rays	Anal spines	Anal rays	Pectoral rays	Pelvic rays	Upper procurrent caudal rays	Upper principal caudal rays	Lower principal caudal rays	Lower procurrent caudal rays	Branchio-stegals
Beryx spp.											
1.0–1.9	0	0	0	0	0	0-0-1	0	0	0	0	0
2.0–2.9	0-I	0	0	0	0	1-1-3	0	0	0	0	0-0-1
3.0–3.9	I-IV-IV	0-0-3	0	0	0	1-2-3	0	0-0-4	0-0-4	0	0-0-5
4.0–4.9	I-IV-IV	0-2-8	0-0-IV	0-0-5	0	2-3-6	0-0-i	0-5-10	0-4-8	0-0-ii	0-4-6
5.0–5.9	IV	3-15	III-IV-IV	5-9-23	0-0-9	2-6	0-iv	9-10-10	8-9-9	0-iii-iv	4-4-5
Beryx splendens											
7.0–7.9	III-IV-IV	14-15	III-IV	28-28-29	15-16-17	5-5-9	iv-v-v	10	9	iv-v-v	5-7
9.0–9.9	IV	13-14-14	III-IV-IV	27-30	17-17-19	6-8	v	10	9	iv-v-v	7-8
10.32	IV	14	IV	29	17	6	v	10	9	v	?
15.00	IV	14	IV	28	19	13	v	10	9	vi	?
21.72	IV	14	IV	28	15	14	v	10	9	v	?
27.58	IV	14	IV	27	17	12	v	10	9	iv	?
Beryx decadactylus											
8.52	IV	18	III	28	14	7	iv	10	9	iv	7
10.08	IV	18	III	28	16	12	v	10	9	iv	?
11.52	IV	18	III	26	17	6	v	10	9	iv	8
16.38	IV	17	IV	26	17	9	v	10	9	iv	8
21.00	IV	18	IV	30	16	11	v	10	9	iv	8
23.28	IV	20	IV	29	16	12	v	10	9	iv	8

spine by 7.5 mm SL. The full adult complement of IV, 26–29 is present by 7.0 mm SL. Pectoral rays develop last, dorsad to ventrad, from 5.9 mm SL on. The full adult complement of 17–18 rays forms by 15 mm SL.

Branchiostegals develop during flexion, at 3.0–6.0 mm (Fig. 2B–D; Table 4). All branchiostegals are formed at 10 mm SL. Scales are developing on one of the two 9.2 mm SL specimens and are completely formed on specimens 15 mm SL and longer.

Pigmentation.—Yolk-sac larvae have unpigmented eyes, and a distinct pattern of melanophores on the forebrain and midbrain, the anterior end of the oil globule, the end of the intestine above the anus, and around the notochord tip (Fig. 1A). As the yolk depletes, the eye becomes pigmented and melanophores appear on the pelvic anlage (Fig. 1B). The pigment on the oil globule becomes incorporated internally above the anterior intestine. This internal pigment eventually lies over the gas bladder (Figs. 1–3). At about 2.0 mm SL, the pigment on the forebrain is incorporated internally as a round spot on one side of the forebrain. This spot is occasionally absent but usually is present on the right side. In the illustrations, this spot is shown on the left side to indicate its presence, but in all illustrated specimens, it actually occurs on the right. By 3.0 mm SL, the pigment around the notochord tip becomes restricted to two small melanophores which disappear when flexion begins (Figs. 1, 2A). The internal pigment over the anterodorsal surface of the gas bladder is present throughout development, although it becomes fainter as the muscles thicken. Internal melanophores are present midway over the intestine only in very few small specimens. An internal pigment spot is present on preflexion and flexion larvae over the hindgut before the anus (Figs. 1D, 2). In postflexion *Beryx,* this spot is elevated as the gas bladder extends posteriad over the hindgut (Fig. 3A) and is absent in specimens larger than 7.0 mm SL (Fig. 3B). An external melanophore over the posterior end of the hindgut is usually present (Figs. 1–3), although it is not seen in some pre- and early flexion specimens. This melanophore is absent or incorporated internally in larvae larger than 6.0 mm SL. Two internal melanophores appear in the otic capsule in larvae larger than 6.0 mm SL. Pigment on the pelvic fins is present in small preflexion larvae (Fig. 1B) and in postflexion specimens (Fig. 3). It is likely that the pelvic rays and membranes are pigmented at all sizes but that the fins were damaged during capture. Larvae larger than 7.0 mm have melanophores at the tip of the elongate dorsal ray. The only external body melanophores of postflexion larvae are on the frontals, over the forebrain.

Juvenile *Beryx* remain pale, with few melanophores (Fig. 4; Abe and Maruyama, 1971; Krefft, 1976), although erythrophores that disappear with preservation give the juveniles a red color (Abe, 1969). A photograph of a freshly caught juvenile *B. decadactylus* (MCZ 61484; 23.3 mm SL) from the Atlantic shows a transparent body, except for silver branchial, otic, and peritoneal regions. The body has a rosy tinge, particularly at the nasal area, along the vertebrae, and along the body margins. The fins are rosy, and the elongate fin rays are red. In overall appearance, the specimen resembles a reddish medusa. Resemblance to coelenterates has been suggested as an explanation for development of elongate fin rays in fish larvae (Govoni et al., 1984; Kendall et al., 1984).

Comparison of Young Beryx decadactylus and B. splendens.—Postflexion and juvenile *B. decadactylus* differ from *B. splendens* only in minor ways (Tables 1–4; Fig. 4). No differences were found in most morphometric features. Body depth, snout-to-eye distance, and snout-to-pelvic distance were greater in *B. decadactylus* than in *B. splendens* >15 mm SL (Tables 1, 2). *Beryx decadactylus* are similar to

B. splendens in head spine development at sizes <15 mm SL. Juvenile *B. decadactylus* (>15 mm SL) have fewer spines on the interopercle, frontal, supraorbital ridge, and dentary. Only the anterolateral ridge of the preopercle has more spines in juvenile *B. decadactylus* than in *B. splendens*. Juvenile *B. splendens* have more accessory spines on the opercular and preopercular spines (Fig. 4).

All specimens of *B. decadactylus* are too large to determine whether the sequence of fin ray formation differs between the two species (Table 4). At present, the difference in dorsal ray count is the only character that allows specific identification of *Beryx* larvae and juveniles.

Pigment differences between the two species are subtle (Fig. 4). *Beryx decadactylus* have more pigment on the peritoneum and branchial region beneath the posterior edge of the gill cover. The latter pigment may prove valuable in distinguishing postflexion *B. decadactylus* from *B. splendens* prior to dorsal ray formation. More specimens of *B. decadactylus* are needed to determine whether this is specific, rather than individual, pigment variation.

Distribution at the Hancock Seamount.—*Beryx* larvae were found almost exclusively in the upper 50 m. They were approximately twice as abundant at 0–25 m than at 25–50 m. Most were captured at night, with no increase in numbers at greater depths during the day; therefore, net avoidance may account for the diel difference in catches.

Larval *Beryx* were found at the Hancock Seamount in July 1984 but not in February 1985 (NMFS, unpubl. data) even though the same collection methods were used. Based on collections of larvae, alfonsin spawn during summer in this region.

SYSTEMATIC IMPLICATIONS

It has often been suggested that the order Beryciformes is not monophyletic (Zehren, 1979; Lauder and Liem, 1983; Keene and Tighe, 1984). For example, the Polymixiidae has been variously excluded from or included in the order, and the Holocentridae has been suggested to be more closely related to perciforms than to other beryciforms (Zehren, 1979). Larval characters may aid in determining the relationships of the beryciform families (Keene and Tighe, 1984).

Larval and juvenile *Beryx* have few character states that can be identified as synapomorphic with other beryciform families. The development of spinous, procurrent caudal rays is one (Lauder and Liem, 1983), although the distribution of this state needs to be surveyed. The juvenile head spines of *Beryx* (Fig. 5) may be informative; recent studies of percomorphs have demonstrated the value of ontogenetic cranial characters in systematics (Johnson, 1984; Johnson and Washington, 1987). The bones of the opercular and pectoral series bear numerous spines, as is common for larval percomorphs (Johnson, 1984). As in many percomorph families (Leis and Rennis, 1983; Johnson, 1984), spines are found along the posterior margin and anterolateral flange of the preopercle. In the circumorbital series, the large spine of the first infraorbital, among the first to develop, persists as large and isolated in adults (Zehren, 1979).

Johnson (1984) has suggested that larval spines of the cranial bones may be among the most useful for elucidating relationships among percomorphs. The frontals of *Beryx* larvae are heavily ornamented. Large anteromedial spines are characteristic of flexion and larger larvae. In addition, the frontals are rugose at relatively small sizes (Table 3). The degree of head spine ornamentation of larval *Beryx* does not approach that seen in many beryciform larvae (Keene and Tighe, 1984). The large spines on the first infraorbital seem to be autapomorphic for the genus. *Beryx* lack the enlarged, serrate supraoccipital crest of the holocentrids (Keene and Tighe, 1984). The holocentrids share this character with the perciform families Scombropidae, Lethrinidae, Cepolidae, Priacanthidae, and Pentacerotidae (Johnson, 1984). *Beryx* larvae also lack the enlarged parietal spines that unite the Anoplogasteridae and Diretmidae (Keene and Tighe, 1984). Among the Melamphaidae, only *Poromitra* has head spination similar to *Beryx*, including frontal spines in *P. capito* (Ebeling and Weed, 1973) and *P. crassiceps* (pers. observ.). The trachichthyids have a complex pattern of small head spines (Keene and Tighe, 1984). Use of larval head spination in the systematics of Beryciformes must await the exact description of those spines in the various families.

Other characters of interest include the shape and coiling of the intestine and the early development of the fins. Again, *Beryx* larvae are most similar to *Melamphaes* in these characters (Keene and Tighe, 1984). Beryciform families with early pelvic fin development include the Anomalopidae, Holocentridae, Melamphaidae, Monocentrididae, and Gibberichthyidae (Keene and Tighe, 1984; Okiyama, 1988; Colin, in press). Larval *Beryx* share with the percoid family Pempherididae not only the early pelvic development, but also the form of the intestine and the persistence of a remnant of the dorsal finfold that resembles an adipose fin in larvae nearing transformation (Leis and Rennis, 1983).

Larval characters will only be useful in beryciform systematics when a thorough survey of character states exists. More importantly, the polarity of these states must be determined at the basal level of the Percomorpha, to avoid the persistent problem of defining groups such as the Beryciformes by plesiomorphic percomorph states. Many larval characters of *Beryx*, such as the spines on the gill cover and the intestine shape, may prove to be plesiomorphic for percomorphs and, therefore, uninformative about the relationships of beryciform families.

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MATERIAL EXAMINED

Beryx spp.: Uncatalogued. 130 (1.3–6.0 mm SL), Hancock Seamount, 29°46.9′–29°48.1′N, 179°02.7′–179°05.3′E, and vicinity, 29°45.0′–29°50.2′N, 178°46.5′–178°56.5′E, 1 m^2 Tucker trawl, 0–50 m, 9–28 July 1984.

Beryx splendens: Uncatalogued. 1 (3.0 mm SL), reared from strip-spawned adults collected at Hancock Seamount, 29°48′N, 179°04′N, handline, 30 July 1984. Uncatalogued. 3 (7.3–7.5 mm SL), vicinity of Hancock Seamount, 29°48.1′–29°54.8′E, 178°49.6′–178°54.8′E, 1 m^2 Tucker trawl, 0–50 m 9–10 July 1988. MCZ 055334. 1 (27.5 mm SL), North Atlantic, 41°31′N, 55°11′W, 10-foot Isaacs-Kidd midwater trawl (IKMT), 22–30 m, 5 September 1964. MCZ 59033. 1 (15.2 mm SL, cleared and stained with alcian blue), North Atlantic, 34°18′N, 75°08′W, 10 m^2 MOCNESS, 70–140 m, 16 August 1978. MCZ 064862. 3 (9.2–10.3 mm SL), North Atlantic, 31°57′N, 77°21′W, 10 m^2 MOCNESS, 0–70 m, 7 August 1978. MCZ 064864. 1 (21.7 mm SL), North Atlantic, 15°30′N, 25°12′W, 10-foot IKMT, 85–95 m, 24 November 1970. MCZ 064865. 1 (7.4 mm SL), North Atlantic, 14°38′N, 50°12′W, 10-foot IKMT, 0–515 m, 10 October 1973. MCZ 068672. 1 (15.0 mm SL), North Atlantic, 30°01′N, 80°10′W, 10m^2 MOCNESS, 0–250 m, 4 August 1978. MCZ 068673. 1 (10.0 mm SL), North Atlantic, 34°15′N, 75°00′W, 10 m^2 MOCNESS, 0–70 m, 14 August 1978.

Beryx decadactylus: ARC 8602986, 1 (11.5 mm SL), North Atlantic, 42°09′N, 63°27′W, pelagic juvenile gadoid trawl (IGYPT), 0–204 m, 27 October 1984. MCZ 061484, 1 (23.3 mm SL), North Atlantic, 40°20.5′N, 50°47.1′W, 10 m² rectangular midwater trawl, 60 m wire out, 16 August 1984. MCZ 064863, 1 (16.4 mm SL), North Atlantic, 31°41′N, 76°58′W, 10 m² MOCNESS, 0–50 m, 31 July 1978. MCZ 064866, 2 (8.5–10.1 mm SL), North Atlantic, 32°10′N, 77°03′W, 10 m² MOCNESS, 0–110 m, 1 August 1978. MCZ 064867, 1 (21.0 mm SL), North Atlantic, 37°37′N, 66°43′W, 10-foot IKMT, 36–36 m, 26 August 1967.

LITERATURE CITED

Abe, T. 1969. Notes on some edible marine fishes collected between the Bonin Islands and the mouth of the Sagami Bay—III. Bull. Tokai Reg. Fish. Res. Lab. 60: 5–8, + pl. 1.

——— and K. Maruyama. 1971. On a young example of *Beryx decadactylus* Cuvier from northern Japan. Bull. Tokai Reg. Fish. Res. Lab. 65: 1–3.

Ahlstrom, E. H., J. L. Butler and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26: 285–402.

———, K. Amaoka, D. A. Hensley, H. G. Moser and B. Y. Sumida. 1984. Pleuronectiformes: development. Pages 640–670 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 1.

Auer, N. A. 1982. Family Percopsidae, trout-perches. Pages 464–469 *in* N. A. Auer, ed. Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission, Ann Arbor, Michigan. Spec. Publ. 82-3.

Busakhin, S. V. 1982. Systematics and distribution of the family Berycidae (Osteichthyes) in the world ocean. J. Ichthyol. 22(6): 1–21.

Colin, P. L. In press. Anomalopidae—lanterneye or flashlightfishes. *In* J. M. Leis and T. Trnski, eds. The larvae of Indo-Pacific shorefishes. New South Wales Univ. Press.

Ebeling, A. W. 1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana-Rep. 58: 164 pp.

——— and W. H. Weed, III. 1963. Melamphaidae II. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. Dana Rep. 60: 58 pp.

——— and ———. 1973. Order Xenoberyces (Stephanoberyciformes). Pages 397–478 *in* D. M. Cohen, ed. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. No. 1 (Pt. 6).

Fourmanoir, P. 1976. Formes post-larvaires et juveniles de poissons côtiers pris au chalut pélagique dans le sud-ouest Pacifique. Cah. Pac. 19: 47–88. (In French)

Fuiman, L. A. 1982. Correspondence of myomeres and vertebrae and their natural variability during the first year of life in yellow perch. Fifth Annual Larval Fish Conference, Louisiana Cooperative Fisheries Research Unit. 56–59.

Govoni, J. J., J. E. Olney, D. F. Markle and W. R. Curtsinger. 1984. Observations on structure and evaluation of possible functions of the vexillum in larval Carapidae (Ophidiiformes). Bull. Mar. Sci. 34: 60–70.

Heemstra, P. C. 1986. Family No. 126: Berycidae. Pages 409–410 *in* M. M. Smith and P. C. Heemstra, eds. Smiths' sea fishes. Springer-Verlag, Berlin.

Johnson, G. D. 1984. Percoidei: development and relationships. Pages 464–498 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1.

——— and B. B. Washington. 1987. Larvae of the moorish idol, *Zanclus cornutus*, including a comparison with other larval acanthuroids. Bull. Mar. Sci. 40: 494–511.

Keene, M. J. and K. A. Tighe. 1984. Beryciformes: development and relationships. Pages 383–398 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1.

Kendall, A. W., Jr., E. H. Ahlstrom and H. G. Moser. 1984. Early life history stages of fishes and their characters. Pages 11–22 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1.

Krefft, G. 1976. Ergebnisse der Forschungreisen des FFS "Walter Herwig" nach Südamerika. XLI.) Fische der Ordnung Beryciformes aus dem Südwestatlantik. Arch. FischWiss. 26: 65–86. (In German, English summary)

Lauder, G. V. and K. F. Liem. 1983. The evolution and interrelationships of actinopterygian fishes. Bull. Mus. Comp. Zool. 150: 95–197.

Lavenberg, R. J., G. E. McGowen and R. E. Woodsum. 1984. Preservation and curation. Pages 57–59 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L.

Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1.

Leis, J. M. and D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales Univ. Press, Sydney. 269 pp.

——— and T. Trnski. In press. The larvae of Indo-Pacific shorefishes. New South Wales Univ. Press, Sydney.

Moser, H. G. and E. H. Ahlstrom. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 7: 1–145.

Okiyama, M. 1988. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo. 1154 pp. (In Japanese)

Olney, J. E. 1984. Lampriformes: development and relationships. Pages 368–379 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol. Spec. Publ. No. 1.

Onishi, K. 1966. Artificial fertilization of the eggs of *Beryx splendens*. Jpn. J. Ichthyol. 16: 27–33. (In Japanese, English summary)

———. 1968. Studies on the early life history of *Beryx splendens*—I. On the morphogenesis and characteristics of eggs and fry by artificial fertilization. Bull. Shizuoka Pref. Fish. Exp. Stn. 1: 17–26. (In Japanese)

Roule, M. L. 1924. Description d'une forme nouvelle d'un poisson appartenant à la famille des Bérycidés. *Actinoberyx jugeati* nov. gen. nov. sp. = ? mutation de *Beryx splendens* C. V.; suivie d'une revision cette famille. Bull. Mus. Nat. Hist. Natur. 30: 68–74. (In French)

Seki, M. P. and D. T. Tagami. 1986. Review and present status of handline and bottom longline fisheries for alfonsin. Pages 31–35 *in* R. N. Uchida, S. Hayasi and G. W. Boehlert, eds. The environment and resources of seamounts in the North Pacific. Proceedings of the Workshop on the Environment and Resources of Seamounts in the North Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

Smith, P. E. and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Pap. 175. 100 pp.

Starks, E. C. 1904. The osteology of some berycoid fishes. Proc. U.S. Nat. Mus. 27: 601–619.

Uchida, R. N. and D. T. Tagami. 1984. Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46: 1–17.

Woods, L. P. and P. M. Sonoda. 1973. Order Berycomorphi (Beryciformes). Pages 263–396 *in* D. M. Cohen, ed. Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. No. 1 (Pt. 6).

Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei). Evol. Monogr. 1. 389 pp.

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Calibrating Dental Layers in Captive ottlenose Dolphins from Serial etracycline Labels and ooth Extractions

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TRODUCTION

ientists studying marine mammal populations
ve become increasingly dependent on age esti-
ates from tooth layer counts to assess the popu-
ion dynamics (Scheffer and Myrick, 1981). Such
pendence has underscored the importance of
derstanding the patterns and rates of tooth
er deposition.

Cetacean teeth have complex patterns of layers,
growth layer groups (GLGs, terminology of
rrin and Myrick, 1981), which are similar to each
ner in detail. The GLG has been assumed to
present deposition during a 1-year period or
me other constant unit of time (Sergeant, 1959).
owever, neither GLGs nor the variably promi-
nt finer layers that they contain can be inter-
eted with certainty until GLG patterns are cali-
ated with units of absolute time.

Rough calibrations of GLGs with absolute time can be achieved by using layers known to have been deposited between two dates (Myrick, 1981a; Myrick *et al.*, 1984; Hohn, Chapter 33, this volume). However, calibration based only on two dates (usually birth and death) gives only a mean annual rate that provides no information on whether the GLG pattern and formation period are dependent on endogenous or exogenous factors. If rates are factor-dependent, then GLGs cannot be used with confidence to estimate ages unless the nature and timing of the factors are known.

Three techniques have been used to calibrate GLGs with two dates. In one, layer patterns were examined in single teeth from a few captive-born (known-age) bottlenose dolphins, *Tursiops truncatus* (Sergeant, 1959; Sergeant *et al.*, 1973; Hui, 1978). In another, a single lead acetate or tetracycline label was introduced into the layering pattern, and tooth layers deposited after the label

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were examined (*Stenella coeruleoalba*, Nishiwaki and Yagi, 1953; *Phocoena phocoena*, Nielsen, 1972; *Lagenorhynchus obscurus*, Best, 1976; and *Delphinus delphis*, Gurevich *et al.*, 1981). In the third, two teeth from a bottlenose dolphin were extracted a few years apart, and the difference in the number of GLGs was noted (Hui, 1978).

The successful uses of these techniques have led to recommendations calling for more sophisticated studies that include combinations of the following: (1) monitoring captive-born animals, whose ages are exactly known, together with wild captives of the same species to compare GLG patterns; (2) introducing tetracycline labels weeks or months apart over several years to mark segments of time in tissue that could be studied alone or with other segments; (3) studying the timing of unique or repeated physical events to determine any association with changes in GLG patterns during a monitored experimental period; and (4) using serial extractions to compare tissue deposition between teeth from one animal as well as between teeth of different animals to detect similarities and differences produced over the same period (Myrick, 1981a,b; Myrick *et al.*, 1984).

In addition, after it was realized that multiple tetracycline labels may be inadvertently produced in teeth of captive dolphins through repeated therapeutic treatments of the animals, Myrick (1981a) suggested studying layering rates retrospectively by matching labels to treatment dates from the medical records maintained by oceanaria. Myrick *et al.* (1984) conducted such a study of seven Hawaiian spinner dolphins (*Stenella longirostris*) (four dead, three living), held at Sea Life Park in Hawaii, that had been treated intermittently with tetracycline for up to 8 years. To ensure that at least some labels could be documented if therapeutic records and labels could not be matched, experimental injections of tetracycline were given and three tooth extractions were made during a 1-year period for each of the three live animals.

The Hawaiian spinner dolphin study showed annual dentinal GLGs to be of age-specific thickness, which varied only slighty from tooth to tooth in each individual and between animals of the same age. Annually deposited dentine revealed that a GLG consists of two light layers, each followed by a dark layer. In addition to the coarse GLG pattern, about 13 pairs of finer layers were visible in annual GLGs, each pair consisting of a dark layer and a light layer. Where fine layers were especially distinct and tetracycline labels closely spaced, label dates showed that a pair of fine layers was formed each month. No differences were noted between the GLG patterns formed while the animals lived in the wild and the patterns formed in captivity. This led to the conclusion that neither the captive environment nor the natural environment influenced dental layering patterns in the specimens studied (Myrick *et al.*, 1984).

In 1979, as part of a continuing effort to examine GLG patterns and deposition rates in delphinids, we began a 3.5-year project to calibrate tooth layers in bottlenose dolphins. Our two objectives were to use multiple tetracycline injections and tooth extractions in captive bottlenose dolphins to monitor rates of tooth tissue deposition, in relation to measurable factors that might affect deposition, and to calibrate GLGs with absolute time. Here we describe the protocol and results of the project.

METHODS AND MATERIALS

The Sample

We used data from 12 bottlenose dolphins (three females and nine males), hereafter called "animals" or "dolphins," maintained for public display at the three parks operated by Sea World, Inc., in San Diego, California (SWSD), Orlando, Florida (SWO), and Aurora (near Cleveland), Ohio (SWA). The dolphins ranged from captive-born yearlings to wild animals that had been held in captivity for up to 9 years (Table 1). All but one of the wild animals were collected from coastal waters off Florida; the other was captured in the Pacific Ocean off California. One of the three females (animal M) died 1 year and 3 months after the project began.

Tetracycline Labeling and Tooth Extractions

Treatments, begun in the spring of 1979, were of four types: tooth extraction and tetracycline labeling, tetracycline labeling only, extraction only, and

Table 1
Background Data and Age Estimates of 12 Captive Bottlenose Dolphins Used in Dental Layer Calibration Project

Animal	Sex	Origin[a]	Date of Birth or Capture	Capture Length/Age or Age By GLG Inspection (Years)[b]	Preproject Time in Captivity (Years)	Age at End of Project (Years)
A	M	cb:P/F	5-78		1.1	4.5
B	M	cb:F/F	5-78		1.1	4.5
C	M	cb:F/P	4-78		1.2	4.6
D	F	wc:F/F	9-77	195 cm/2	1.8	7.2
E	M	wc:F/F	1-77	201 cm/2	2.3	8.0
F	M	wc:F/F	10-75	2	3.7	8.5
I	F	wc:F/F	6-70	1–2*	9.0	14.0
J	M	wc:F/F	12-72	3–4*	6.4	13.0
M	F	wc:F/F	2-79	196 cm/2	0.3	3.0[c]
P	M	wc:P/P	2-78	3*	1.3	7.0
Controls						
K	M	wc:F/F	12-72	1–2	6.4	11.0
L	M	wc:F/F	11-72	4	6.5	14.0

[a] cb, Captive born; wc, wild captured; P/F or F/P, hybrid; origin of mother/sire; P/P, Pacific purebred; F/F, Florida coastal purebred.

[b] An asterisk indicates that age was estimated based on GLG counts relative to label introduced at capture.

[c] Animal M died in the second year of the project.

handling (i.e., sham procedures) only. Biomycin, a tetracycline, was the labeling agent used; it was injected into the dorsal musculature slightly off the midline of the body and anterior to the dorsal fin, at a dosage of 20–30 mg/kg body weight. Teeth were extracted from the middle of the row of either lower jaw using anesthetization and extraction methods similar to those described by Ridgway *et al.* (1975) and used successfully on Hawaiian spinner dolphins by Myrick *et al.* (1984).

Each animal had one tooth extracted and received one injection at the beginning of the study. All except the two animals (K and L) that were used as controls received tetracycline injections approximately every 3 months and had one or (occasionally) two teeth extracted each year for the next 3.5 years. All intact teeth were permanently labeled each time tetracycline was injected. A label introduced after the first tooth was extracted appeared in the second and third teeth and so on, but not in the first tooth (Table 2). In sham procedures, dolphins were lifted out of the water, weighed, measured, and returned to the pool. Sham procedures were done at random in lieu of real treatment or extraction to determine whether merely removing an animal from the water and weighing and measuring it affected its tooth-layering patterns.

The two control animals were not experimentally treated after the initial treatment and extraction at the start of the project. A second tooth was extracted from them only at the termination of the experiment (fall 1982) when a final extraction was carried out on all animals involved in the project.

Dolphin Health and Environment

We recorded average weekly changes in water temperature and salinity, and the average daily amount and species of food consumed by each animal, to identify any effects of these factors on dental-layering pattern or deposition rate (water

Table 2
Extraction and Labeling Schedule for Animal F as an Example of How Serial Data Were Generated for Analysis

Date or Period	Tooth Extracted	Labels Present	Labels Introduced
6-5-79	F1	None	A
9-7-79			B
9-11-79 to 10-9-79 daily			C (therapeutic)
11-1-79 to 11-4-79 daily			D (therapeutic)
12-3-79			E
3-10-80			F
5-28-80	F2	A through F	G
9-5-80			H
12-4-80	F3	A through H	I
12-10-80			J (therapeutic)
3-5-81			K
6-9-81			L
9-8-81			M
12-14-81	F4	A through M	N
1-15-82			O (therapeutic)
3-5-82			P (therapeutic)
6-4-82			Q
9-7-82			R
1-11-82	F5[a]	A through R	None

[a] Last tooth extracted; end of project.

temperatures and salinities were artificially controlled at Ohio and Florida parks). In addition, daily records were made of behavior, including type of activity (e.g., free feeding, training, show), periods of illness and treatment, and within-park transfers from one tank or pool to another. Finally, because SWA is 11° latitude farther north than SWSD and 14° latitude farther north than SWO, we tracked transfer of dolphins between parks (interpark transport) to try to detect possible effects of long-distance transport or changes in latitude on dental-layering patterns.

Tooth Preparation and Examination

Preparation and examination of teeth followed the methods described by Myrick *et al.* (1983). Each tooth was prepared in untreated mid-longitudinal thin section between approximately 100 and 150 μm thick. In a few cases, decalcified and hematoxylin stained thin sections, about 40 μm thick, were prepared from the remaining fragments (leftovers) to enhance resolution of layering patterns. Microscopic examination was in plain and polarized transmitted light to determine layering structure and in UV reflected light to locate tetracycline labels, visible as fluorescent lines (Fig. 1A,B).

The best sections of the series of teeth extracted from each animal were photographed in plain and UV light, and their interstructural (e.g., between the neonatal line and the pulp-cavity margin) and interlabel distances were measured. Distance measurements (in micrometers) were taken in a step-down fashion toward the pulp cavity from the neck region of the tooth near the base of and perpendicular to the neonatal line (Fig. 1B; see

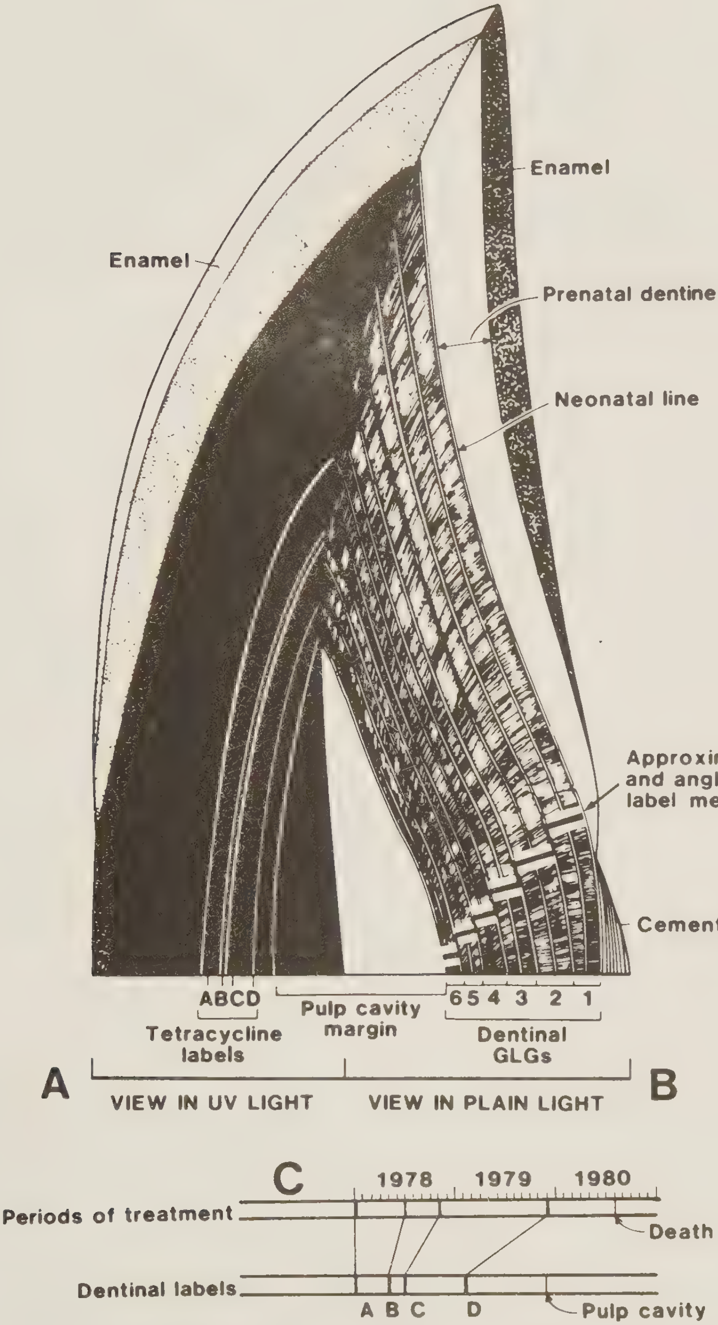

Enamel
Enamel
Prenatal dentine
Neonatal line
Approximate region and angle of GLG and label measurements
Cementum
ABCD
Tetracycline labels
Pulp cavity margin
6 5 4 3 2 1
Dentinal GLGs
A
B
VIEW IN UV LIGHT
VIEW IN PLAIN LIGHT
C
1978
1979
1980
Periods of treatment
Death
Dentinal labels
A B C
D
Pulp cavity

Figure 1 Diagram of tooth thin section from hypothetical project dolphin showing tetracycline labels, A–D under ultraviolet light (A, left-hand side) and dentinal growth layer group (GLG) layering patterns under plain light and standard positions in tooth where labels and GLGs are measured (B, right-hand side). (C) Method of identifying labels introduced into tooth and determining elapsed time between labels by comparing relative spacing of labels. (Modified from Myrick *et al.*, 1984.)

also Myrick *et al.*, 1984). (In this region the layers are usually the least distorted, neither highly expanded as in the apex, nor strongly narrowed as in the root base.)

The mean of three to five series of measurements was used for final values of GLG thickness (Table 3). Each series of thickness measurements was taken at a different time to minimize measurer bias. At least one full series of measurements was taken from the last tooth pulled from an animal because it contained the complete continuous record of the project period. Because the full 3.5-year monitored record had not been completed in teeth extracted before the end of the project, measurements taken from such teeth were augmented by measurements from teeth that were extracted later in the project, including the last tooth extracted. This helped to ensure, as well as possible, that GLG and interlabel distances in most of the teeth extracted from each animal were represented in calculating final mean values.

Data Analysis

Label locations on the UV micrographs were marked on clear plastic overlays, which were then aligned on the corresponding plain light micrographs to determine the location of the labels among the layers. Label positions for each animal were transcribed onto a calibration chart as a row of vertical lines, each separated from others and tooth landmarks (such as the neonatal line) on a scale representing 10-μm intervals. Above this row of label distances, the treatment and extraction data were transcribed as a row of lines scaled in months, representing time of treatment. The two data rows completed for each animal were used to identify corresponding project treatments and labels, designated alphabetically in the order that they were introduced (Fig. 1C).

Time-Calibrated Dentinal Patterns

To define annual or subannual depositional segments within the dentinal patterns, distance measurements between labels spanning a year or half-years were added together. Because the animals were often treated on different days or months, spaces between labels in the teeth represented various lengths of time. These different time-calibrated segments provided many opportunities to examine layering patterns in the continuum within 3.5 years of monitored deposition. Repeating patterns of yearly deposition could be identified, annual GLGs could be defined, and time represented by GLG component (fine) layers could be investigated.

Monthly Depositional Rates

There were enough data points from most of the dolphins to calculate average monthly depositional rates by dividing segment distance (in micrometers) by elapsed time of segment deposition. Although all twelve project animals were useful in determining annual GLGs, only eight of the twelve animals were useful in studying monthly rates. This was because the two controls did not have enough labels, and in one other animal (J) distances between labels were so short that measurements lacked precision. For the fourth animal (M, which died after 1 year and 3 months), the period was too short to yield enough data. For each of the eight measurable animals, average monthly depositional rates were compared with season, water temperature, and salinity data, and with periods of illness, behavior and feeding, and interpark transport.

Calibration of Preproject Layers

Because nine of the animals were captured at about 2 years old or older, the earliest formed layers were accumulated before capture and it was not possible to calibrate those GLGs directly. We characterized the patterns of initial GLGs exhibited in the three captive-born animals (A, B, and C), which, by the end of the project, had four and a half completely documented GLGs. However, we were reluctant to use these patterns before interpreting initial annual GLGs in the remaining animals for three reasons: (1) two of the captive-born dolphins were hybrids (mother and sire were from different populations), and it was not known whether hybridization affected dentinal-layer patterns; (2) all three had always been in captivity,

Table 3
Number and Mean Thickness (μm) of Completed Annual Growth Layer Groups in Dentine of 12 Captive Bottlenose Dolphins[a]

	GLG Number														
Animal	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M	900*	500*	343												
	(41)	(44)	(69)												
	4	4	5												
A	858	536	458	461	( )										
	(38)	(56)	(19)	(11)											
	4	3	3	3											
B	881	500	348	375	( )										
	(22)	(56)	(38)	(21)											
	4	4	4	4											
C	471	327	298	281	( )										
	(13)	(15)	(5)	(13)											
	5	5	5	5											
D	825*	500*	370*	340*	234	239	190	( )							
	(35)	(0)	(28)	(14)	(11)	(18)	(10)								
	3	3	3	3	5	5	5								
P	505*	375*	350*	339*	352	350	337	( )							
	(10)	(50)	(0)	(14)	(22)	(35)	(32)								
	4	4	4	4	4	3	3								
E	875*	500*	425*	347*	300*	303	215	211	( )						
	(29)	(0)	(25)	(42)	(35)	(16)	(11)	(14)							
	4	3	5	4	5	5	5	4							
F	925?	500?	450?	375?	300?	195	291	191	( )						
	(29)	(0)	(0)	(29)	(0)	(31)	(41)	(53)							
	4	3	3	4	3	5	5	5							
I	813*	465*	440*	360*	300*	280*	225*	195*	180*	185*	170*	185	245	237	( )
	(35)	(21)	(10)	(10)	(0)	(0)	(15)	(15)	(0)	(25)	(65)	(39)	(66)	(32)	
	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
J	890*	463*	450*	407*	353*	293*	230*	220*	207*	187*	167	140	143		
	(17)	(12)	(0)	(23)	(25)	(12)	(10)	(20)	(12)	(12)	(29)	(10)	(12)		
	3	3	3	3	3	3	3	3	3	3	3	3	3		
Controls															
K	817?	520?	450?	373?	320?	240?	237?	182?	160	137	(117)	( )			
	(58)	(27)	(0)	(58)	(35)	(30)	(35)	(17)	(10)	(15)	(6)				
	3	3	3	3	3	3	3	3	3	3	3				
L	820?	483?	450?	417?	407?	367?	283?	263?	243?	170?	170?	150	130	125	
	(27)	(29)	(0)	(58)	(51)	(29)	(29)	(47)	(60)	(17)	(17)	(0)	(0)	(0)	
	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
Florida coast averages (A, B, D, E, F, I, J, K, L, M) (up to 14 GLGs)															
	862	497	418	384	316	274	239	210	198	170	156	158	173	181	
	(40)	(23)	(46)	(39)	(54)	(55)	(36)	(30)	(36)	(23)	(26)	(24)	(63)	(80)	
Pacific coast averages (C, P) (7 GLGs in one of two)															
	488	351	324	310	352	350	337								
	(24)	(34)	(37)	(41)	(0)	(0)	(0)								

[a] ?, Estimated annual GLG by inspection plus time in captivity; *, estimated annual using some documentation; empty parentheses indicate additional partial GLG present; values are means calculated from three to five measurements of GLG thickness; parenthetical values are rounded standard deviations of mean values; third row of values for each specimen is number of measurements used to calculate the mean.

and the effects of captivity were not known; and (3) the dentinal thicknesses of the first three GLGs in one (animal C) of the two hybrids was obviously different from those of the other two captive-born animals (A and B).

To try to calibrate preproject and precapture GLGs of the wild animals, we used estimated age at capture based on capture body length, or on increasing body lengths during the project, plus time in captivity to get a total age in years. (We knew that each animal must have been at least 1 year old when captured and thus the preproject age would have had to be at least 1 year plus total time in captivity.) We then looked for the same number of repeating layer groups as our age estimate. If our GLG count was one or two different than the age in years estimated for a young animal based on body length, we concluded that the body-length age was incorrect and that the GLGs were annual units. For a hypothetical example, based on a capture body length of about 225 cm, an animal estimated to be 3 years old is held captive for 1 year before its first label is introduced. Its teeth should have approximately four repeating GLG units between the neonatal line and the first project label. If only three GLGs occur, we would have to consider the capture-length age estimate of 3 years at 225 cm too high.

In some cases, we tried to augment the calibration of preproject layers by also using certain undocumented labels to define annual preproject GLGs. Here, we assumed that the label closest to the neonatal line and formed before the project began had been introduced at about the time of capture. We hoped to determine whether the number of GLGs formed prior to and after the "capture label" corresponded to age (in years) based on length at capture and time in captivity, respectively (Table 1).

When we decided that the first preproject label in a tooth was introduced at or near the time of capture (as was done in three of five animals), we used the label with the other, better documented labels from project treatments to calibrate all dentine, by inspection, behind and in front of the label. (In a case where the undocumented label was close to the first project label and the animal was captive for several years, we regarded the undocumented label as not a capture label, and calibration by this method was not attempted.) After preproject GLGs were defined in wild specimens by this method, we compared their thicknesses and patterns with those of the three captive-born animals to determine what similarities and differences existed. Adding the three captive-born dolphins to the animals with useful presumed capture labels brought to six the number of animals for which the initial GLGs were defined. We defined initial GLGs in the remaining six animals by inspection, estimated age at length, and time in captivity.

RESULTS AND DISCUSSION

Tetracycline Labels

Preproject Labels

Examinations of sections of the extracted teeth from captive-born dolphin C revealed a fluorescent label in the postnatal dentine approximately 25 μm from the neonatal line in the direction of the pulp cavity (Fig. 2A, C). This male calf was about 3 weeks old and nursing when its mother became sick and was placed on a 10-day treatment of 5 g of tetracycline daily. The closeness of the label to the neonatal line in animal C's teeth is evidence that tetracycline was transferred from mother to calf through the milk during the 10 days of treatment. It is also compatible with the popular assumption that the neonatal line is formed near the time of birth (Nishiwaki and Yagi, 1953; Myrick, 1981b). The calf was never given tetracycline before the project and could not have ingested medicated fish intended for other dolphins sharing the pool because he could not yet eat solid food.

In addition to the label produced in C through nursing, labels introduced before the start of the project were found in the teeth of five of the wild project animals, dolphins I, J, K, L, and P. There were no medical records of tetracycline treatment to account for these labels. Nevertheless, the earliest formed label in each of the three other noncontrol animals (I, J, and P) was used as though it had been introduced at or about the time of the animal's capture (Table 1). This was done to see if estimates of age at capture plus time in captivity in

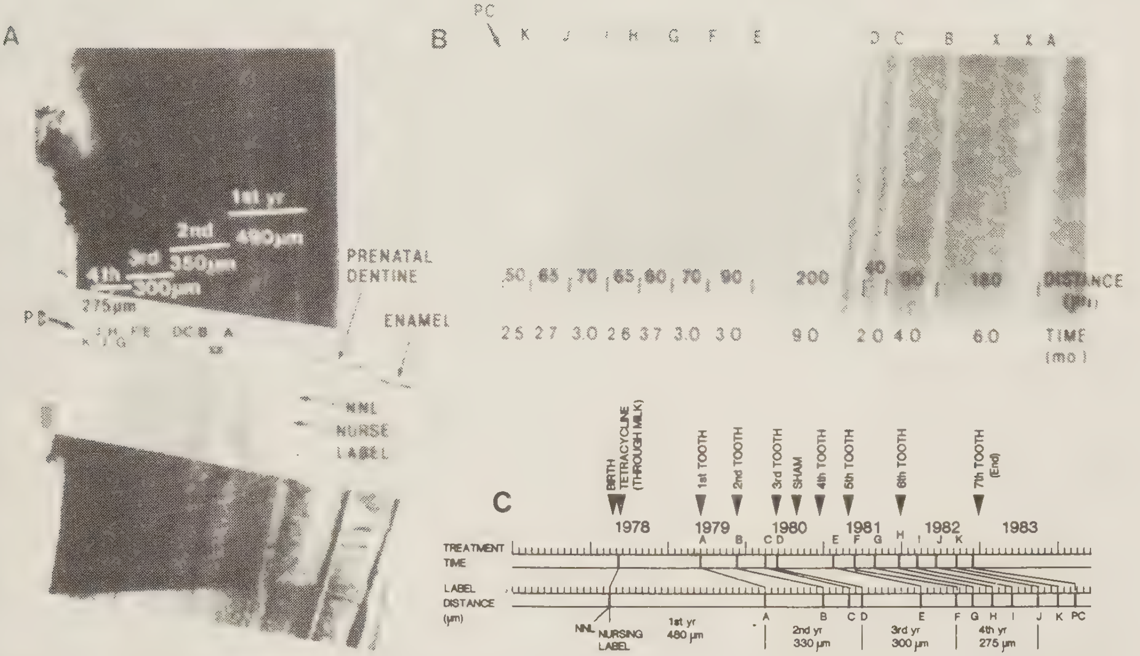


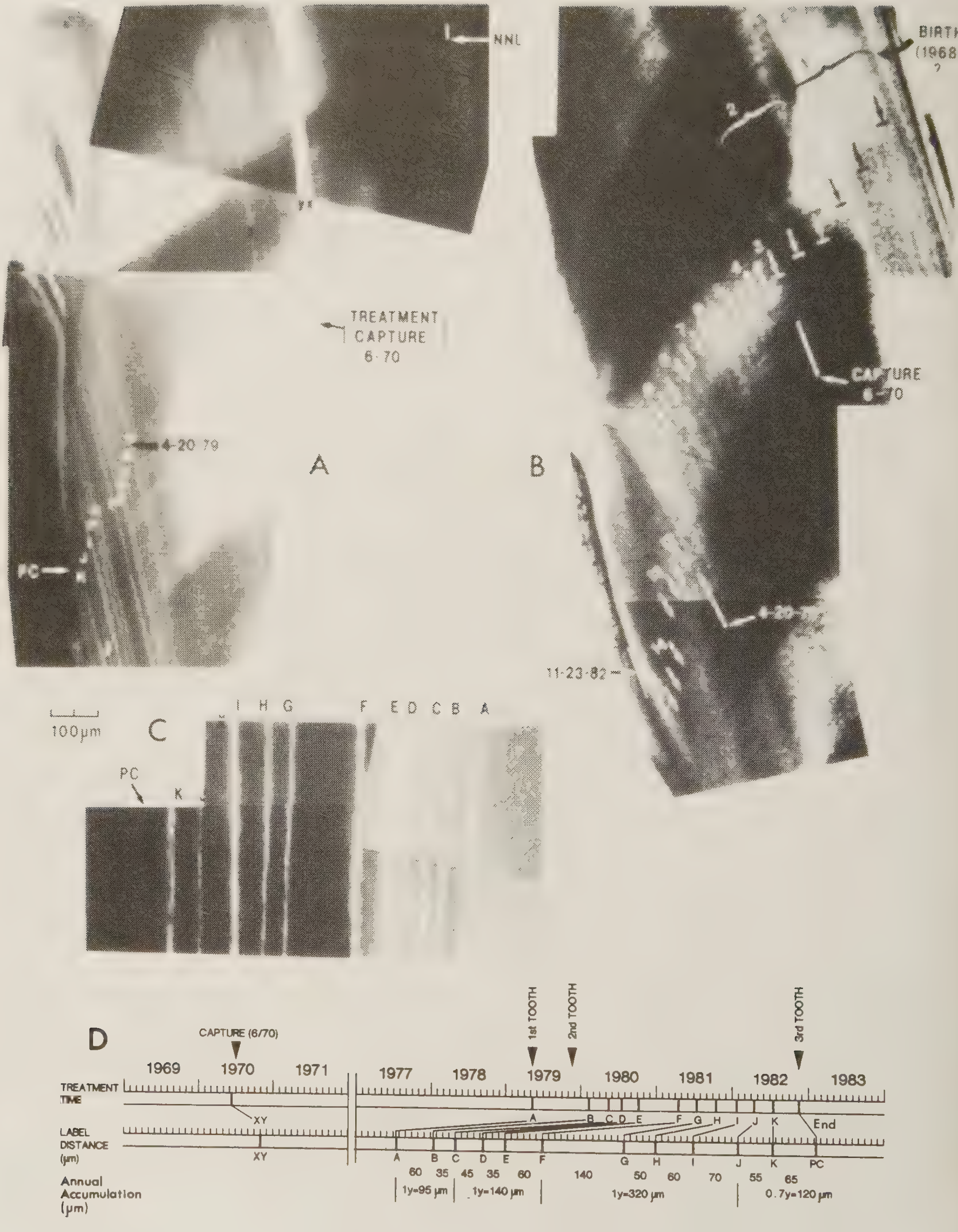
Figure 2 Dentine calibration of animal C. (A) Swatch of UV micrograph with tetracycline labels (lettered) superimposed on light micrograph of dentinal pattern (GLGs marked and measured); ×39. Nurse label internal to the NNL reflects introduction of tetracycline imparted by the mother through milk at 3 weeks after birth. Distance between the NNL and label A is the thickness of dentine deposited in the first 1.1 years. Faint labels between A and B and marked with X are without records. (B) Magnified (×150) UV micrograph of labels showing distances (micrometers) between labels (lettered) and time elapsed between labels (months). (C) Calibration chart showing labeling treatments and tooth extractions, label identifications, and annual dentinal thicknesses. (Abbreviations in this and other figures: PC, pulp-cavity margin; mo, months; yr, year; End, termination of project; 1st TOOTH, 2nd TOOTH, etc., tooth extractions; NNL, neonatal line formed at birth.)

years matched the number of GLGs defined in thickness and pattern that were counted in front of and behind the label.

Preproject labels were not used to estimate age at capture for the two control animals (K and L). This decision was made for animal K because its tooth layers lacked clear patterns in regions critical to interpretation of the labels. The two preproject labels in the teeth of L were too close to the project label (<300 µm), given the animal's 6.5 years in captivity, to have been introduced at capture.

For animal I, a pair of bright, closely spaced labels (X and Y, Fig. 3) occurred about two GLGs inward from the neonatal line (formed at birth) and nine GLGs external to the first project label introduced 20 April 1979. If the XY label is taken as having been introduced at or near capture, June 1970, the project would have begun approximately nine annual GLGs later, which is what the layering pattern showed. Accordingly, animal I would have been about 2 years old at capture, and birth would have been in 1968 (Fig. 3B, D).

For animal J, the presumed capture label was separated from the first project label (A, produced 11 April 1979) by six GLGs, which if formed annually would be compatible with our interpretation that the undocumented label was introduced at capture (December 1972) (Table 1). For animal P, we estimated that the preproject label (X, Fig. 4) was introduced at or about the time of capture for the following reasons. First, P was captured in February 1978 (Table 1), only slightly more than a year before the project began. Second, label X was slightly more than one GLG external to the first


NNL
TREATMENT
CAPTURE
6·70
4-20-79
PC
A
B
BIRTH
(1968)
?
2
CAPTURE
6-70
11-23-82
100µm
C
PC
K
I H G
F E D C B A
D
CAPTURE (6/70)
1st TOOTH
2nd TOOTH
3rd TOOTH
1969 1970 1971
1977 1978 1979 1980 1981 1982 1983
TREATMENT TIME
XY
A B C D E F G H I J K End
LABEL DISTANCE (µm)
XY
A B C D E F G H I J K PC
Annual Accumulation (µm)
60 35 45 35 60 140 50 60 70 55 65
1y=95 µm
1y=140 µm
1y=320 µm
0.7y=120 µm

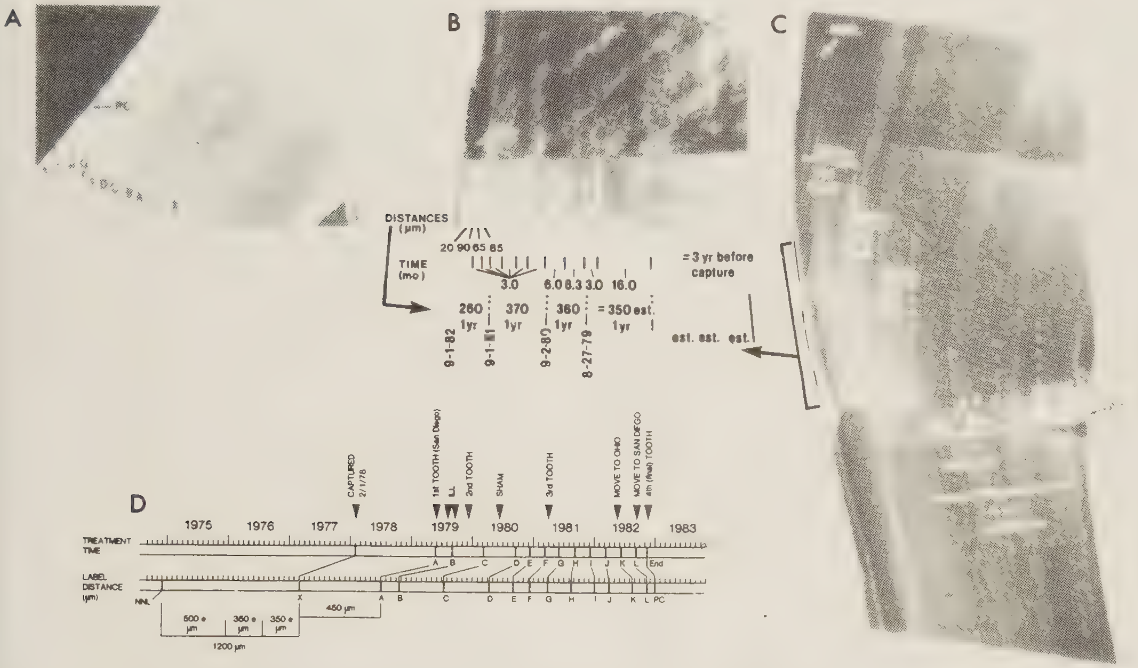

A
B
C
DISTANCES (μm)
20 90 65 85
TIME (mo)
3.0
6.0 6.3 3.0 16.0
260 1yr
370 1yr
360 1yr
= 350 est. 1yr
= 3 yr before capture
est. est. est.
9-1-82
9-1-81
9-2-80
8-27-79
D
CAPTURED 2/1/78
1st TOOTH (San Diego)
LL
2nd TOOTH
SHAM
3rd TOOTH
MOVE TO OHIO
MOVE TO SAN DIEGO
4th (final) TOOTH
1975
1976
1977
1978
1979
1980
1981
1982
1983
TREATMENT TIME
A B C D E F G H I J K L End
LABEL DISTANCE (μm)
NNL
X
A B C D E F G H I J K L PC
450 μm
500 e μm
360 e μm
350 e μm
1200 μm

Figure 4 Dentine calibration of animal P augmented by a capture label. (A) UV micrograph showing all labels including one, X, introduced before the beginning of project, probably at about capture. (B) Light micrograph with swatch of UV micrograph showing positions, distances (in micrometers), and time (in months), and estimated annual depositional thicknesses. (C) Position of labeled portion of dentine and total presumed annual GLGs (marked by dashed lines) in last tooth extracted. Based on project body length increases, P was about 3 years old when captured. (D) Calibrated labels and estimated annual GLG thicknesses deposited before the project label (label A). (Original magnification of A and B, ×150; C, ×39. e, Limits of annual GLGs estimated by inspection and consideration of preproject labels and background data; see Fig. 2 for other abbreviations.)

project label (A). Third, the distance of label X from label A was about the same as or slightly greater than the distance between successive project labels representing almost the same amount of elapsed time. Finally, four GLGs occurred between the neonatal line and the first project label (A), and the body length of P, when label A was introduced, was 268 cm (length continued to increase through the project period to 284 cm). The length at the beginning of the project indicates that of a juvenile of about 4 years old (Table 1).

Thus, there is support, from the three specimens in which the earliest preproject label was assumed to have been introduced at capture, that GLGs defined in this study represent annual

Figure 3 Dentine calibration of animal I. (A and B) UV and light micrographs, respectively, of final extracted tooth (pulled 11-23-82). Three preproject labels (X, Y, Z) are contained in the dentine. Labels XY may have been introduced at or about the time of capture considering the number of apparent GLGs (i.e., double dark and light layer pairs) between the XY labels and the neonatal line and between the labels XY and A, introduced at the beginning of the project, 4-20-79, for this animal. This estimate would be compatible with the capture date of June 1970 given by park records. Numbered paired arrows indicate paired dark layers in the second GLG; triple arrows point out three dark layers in GLG number one. (C and D) The gap between labels F and G is unexpected and represents a break in the rather regular deposition rate. Label X is a faint label without a record. (See Fig. 2 for other abbreviations.)

units. Nonetheless, whether the labels we used actually represented treatments at or near capture is not directly proved.

Intentional Project Labels

In all specimens, all intentionally introduced tetracycline labels were identified in the dentine (e.g., Figs. 2, 3, 4, and 5) but not in the cementum. Apparently the tetracycline doses (20–30 mg/kg body weight) used to label dentine were too weak to produce distinct cemental labels. Because of this, we concentrated mainly on calibrating dentinal layers, and only when strong therapeutic concentrations of tetracycline had been used were labels in dentine and cementum compared.

Therapeutic Project Labels

Labels other than those scheduled in the project were inadvertently introduced when tetracycline was used medicinally during ill health of some of the animals. These therapeutic treatments occurred in the teeth as exceptionally bright, wide labels (e.g., Fig. 5B). We used them as additional data points and to demarcate tissue formed during sickness and recovery.

Unidentified Project Labels

Dolphins A, C, and I each had undocumented labels, introduced during the project, that were much fainter and more irregularly spaced than

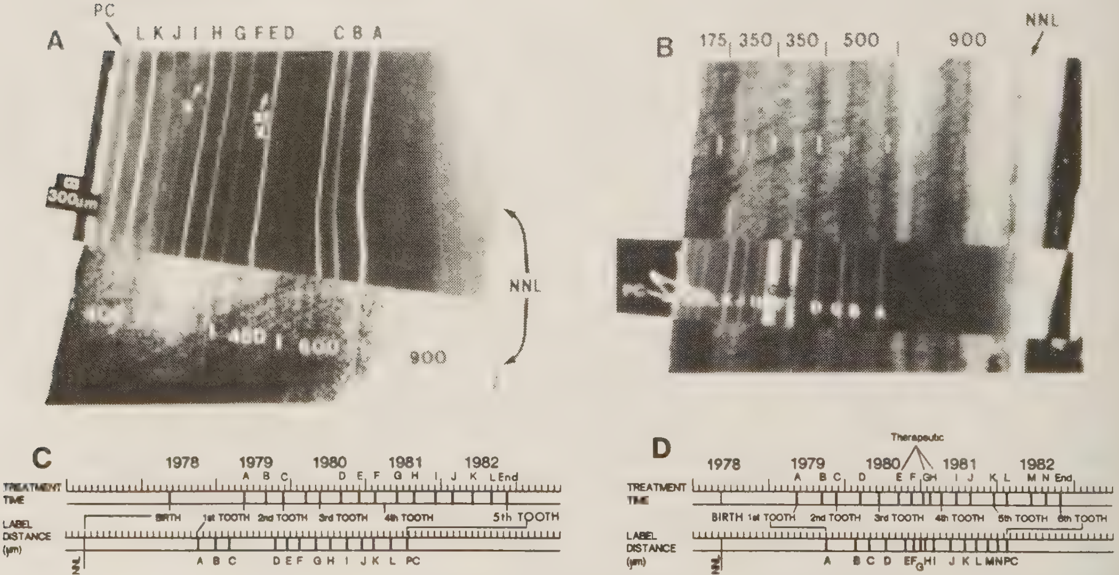

A
PC
L K J I H G F E D C B A
300µm
NNL
400
400
600
900
B
175
350
350
500
900
NNL
C
1978
1979
1980
1981
1982
A B C
D E F G H
I J K L End
TREATMENT TIME
BIRTH
1st TOOTH
2nd TOOTH
3rd TOOTH
4th TOOTH
5th TOOTH
LABEL DISTANCE (µm)
NNL
A B C D E F G H I J K L PC
D
Therapeutic
1978
1979
1980
1981
1982
A B C D E F GH I J K L M N End
TREATMENT TIME
BIRTH
1st TOOTH
2nd TOOTH
3rd TOOTH
4th TOOTH
5th TOOTH
6th TOOTH
LABEL DISTANCE (µm)
NNL
A B C D EF G HI J K L MNPC

Figure 5 Dentinal calibration for animals A and B. (A and B) UV micrographs with tetracycline labels (lettered) superimposed on GLG patterns (measurements) of the final tooth extracted from animals A and B, respectively. (B) White vertical bars indicate the tripartite nature of first (900-m-thick) GLG and bipartite nature of subsequent GLGs. Faint labels indicated by X's in A are without dates. (C and D) Calibration charts for animals A and B with dated tetracycline labelings and tooth extractions connected with labels, lettered in order of introduction. The substantial gap between labels C and D in micrograph A reflects protracted period, shown in chart C, during which no tetracycline was administered to animal A. Chart D for animal B indicates therapeutic treatments of tetracycline as evidenced by thick, bright labels E, G, and H shown in micrograph B. (Original magnification of photos, ×39. See Fig. 2 for abbreviations.)

other labels (Figs. 2A, 3C, and 5A). Because all intentional labels were accounted for in these specimens, we ignored the faint labels. Presumably the labels were formed when the animals ingested fish medicated with tetracycline, intended for other dolphins sharing a common tank. A similar case was reported by Myrick *et al.* (1984) in their study of tetracycline-labeled Hawaiian spinner dolphins.

Dentinal Growth Layer Groups

Untreated Sections

In transmitted light, well-prepared untreated sections of teeth from all project animals had a repeating pattern of layers comprising a GLG similar to those described by Myrick *et al.* (1984) for Hawaiian spinner dolphins. Except for the first-formed GLG, which exhibited three pairs of layers when resolution was adequate, a GLG consisted of two light layers each followed by a darker layer. The more external light layer formed the outer boundary of the GLG, and the second light layer usually was found about midway through the GLG (i.e., "mid-GLG layer," Myrick *et al.*, 1984). Each new GLG began with a light boundary layer formed at the internal margin of the second dark layer of the previous GLG; the dark layer usually highlighted the light boundary layer (Figs. 3B and 5B).

Decalcified and Stained Sections

Because leftovers from the sides of a central untreated section were used to produce decalcified and stained thin sections, most were noticeably off-center, and few were of sufficiently high quality for detailed GLG thickness comparison with their untreated counterparts. The best specimens showed GLGs with thin, dark-stained boundary and mid-GLG layers and a more lightly stained background (Fig. 8A).

The first GLG consisted of three pairs, instead of two pairs, of thin, dark-stained layers and thick, light-stained layers. The two-pair pattern was common in the dentine formed after the first GLG. However, in some cases, the GLG boundary layer was indistinct because one or more thin, dark-stained accessory layers occurred nearby [e.g., note the boundary layer(s) between GLGs 4 and 5 in Fig. 8A].

Calibration of Growth Layer Groups

Age-Specific Growth Layer Group Thickness

Mean thicknesses of GLGs in the 12 animals are presented in Table 3 along with rounded standard deviations. In comparisons of thickness between GLGs, annual dentine deposition had decreased with increased age in all 12 of the project dolphins. Additionally, serial measurements showed that each annual dentinal GLG was deposited at a more or less predetermined thickness according to the age of the animal.

The age-specific GLG thickness pattern (especially for the first three GLGs) was similar in all wild animals from the same geographic area whether the layers were formed in captivity or in the wild. All wild dolphins had already formed at least two GLGs before capture, and the teeth of two captive-born dolphins exhibited GLG thicknesses similar to the Florida specimens. The other captive-born dolphin (animal C) had GLG thicknesses resembling those of the wild animal (P) from California.

Population-Specific Patterns

Comparisons of mean age-specific dentinal thicknesses for the 12 individuals shown in Table 3 indicate the possibility that two depositional patterns exist: one for Florida-coast animals and one for California-coast animals. All wild Florida-coast animals deposited more than 800 μm of dentine the first year, more than 450 μm the second year, and usually more than 350 μm (418 μm average) the third year. This was also true of the captive-born Florida purebred (animal B) and the captive-born hybrid of a Florida male and a Pacific-coast female (animal A) (refer to Table 1). The one wild animal from California (P) apparently deposited about 500, 375, and 350 μm of dentine in his first, second, and third years, respectively. The captive-born hybrid (C) sired by a purebred California male shows a dentinal-depositional pattern (i.e., 471, 327, and 298 μm) much nearer that of animal P than those from Florida animals (Table 3 and Fig. 6).

The Pacific-coast sample ($n = 2$, including animal C) was too small for conclusive results. Nonetheless, it is at least interesting that a thickness pattern so different from the other 10 project animals was found in the wild specimen from California and the one captive-born hybrid male sired by a wild California animal. Figure 6 includes mean values and standard deviations for GLGs one and two. In these GLGs, the two specimens have values more than three standard deviations below mean values of the Florida-coast animals. This indicates that the probability of these two patterns being part of the same population is very low; for the first GLG the probability that the two patterns are from the same population is less than 1.0%.

Monthly Layers

Labels were spaced closely enough and fine dentinal layering was clear enough in several specimens (especially in B, D, and F) to investigate the timing of what have been thought to be monthly layers (e.g., Laws, 1962; Kasuya, 1977; Myrick, 1979) or lunar monthly layers (Myrick, 1981b; Myrick *et al.*, 1984). In the second extracted tooth of D, labels A and B had been introduced 3 months apart, and 3 additional months were represented between label B and the pulp-cavity margin (Fig. 7). Almost four full layers occurred between labels A and B, and there were three layers between label B and the edge of the pulp cavity. In the third extracted tooth of animal D, 12 months were represented between labels A and D. Thirteen pairs of dark–light layers were visible within that segment. In the sixth (last) tooth taken from D, further deposition of monthly layers was identified by comparing layers with elapsed time between labels on the calibration chart (Figs. 7 and 8). In other animals, tooth sections with well-developed fine layering show similar results. This supports calibration observations made earlier by Myrick *et al.* (1984) that fine dentinal layers in dolphins are deposited with lunar (or at least monthly) regularity. Thus, monthly layers have now been verified for time in specimens of two species, Hawaiian spinner dolphins and bottlenose dolphins.

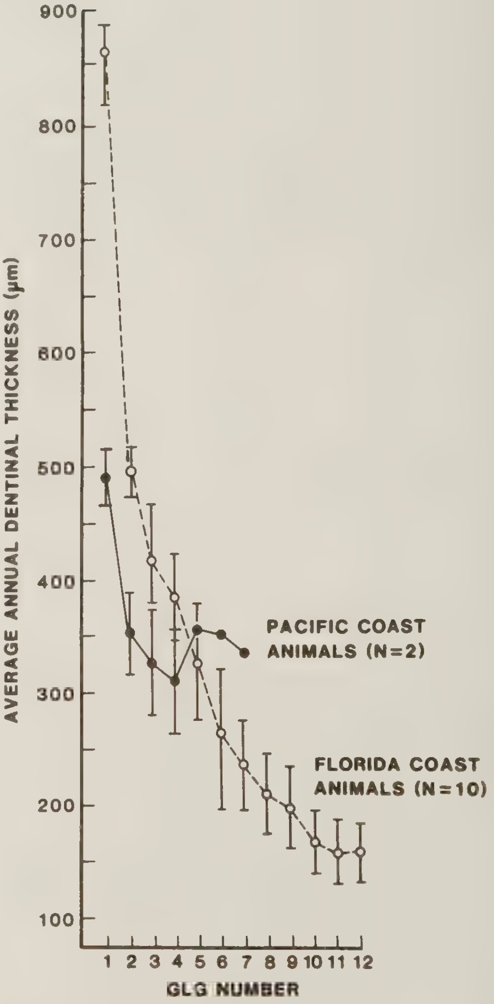


Figure 6 Average dentinal GLG thickness in Pacific-coast and Florida-coast bottlenose dolphins. Vertical lines represent one standard deviation from mean values.

Monthly Rates of Deposition

Enough between-label measurements were available to plot mean monthly accumulated thicknesses (in micrometers) of dentine during the

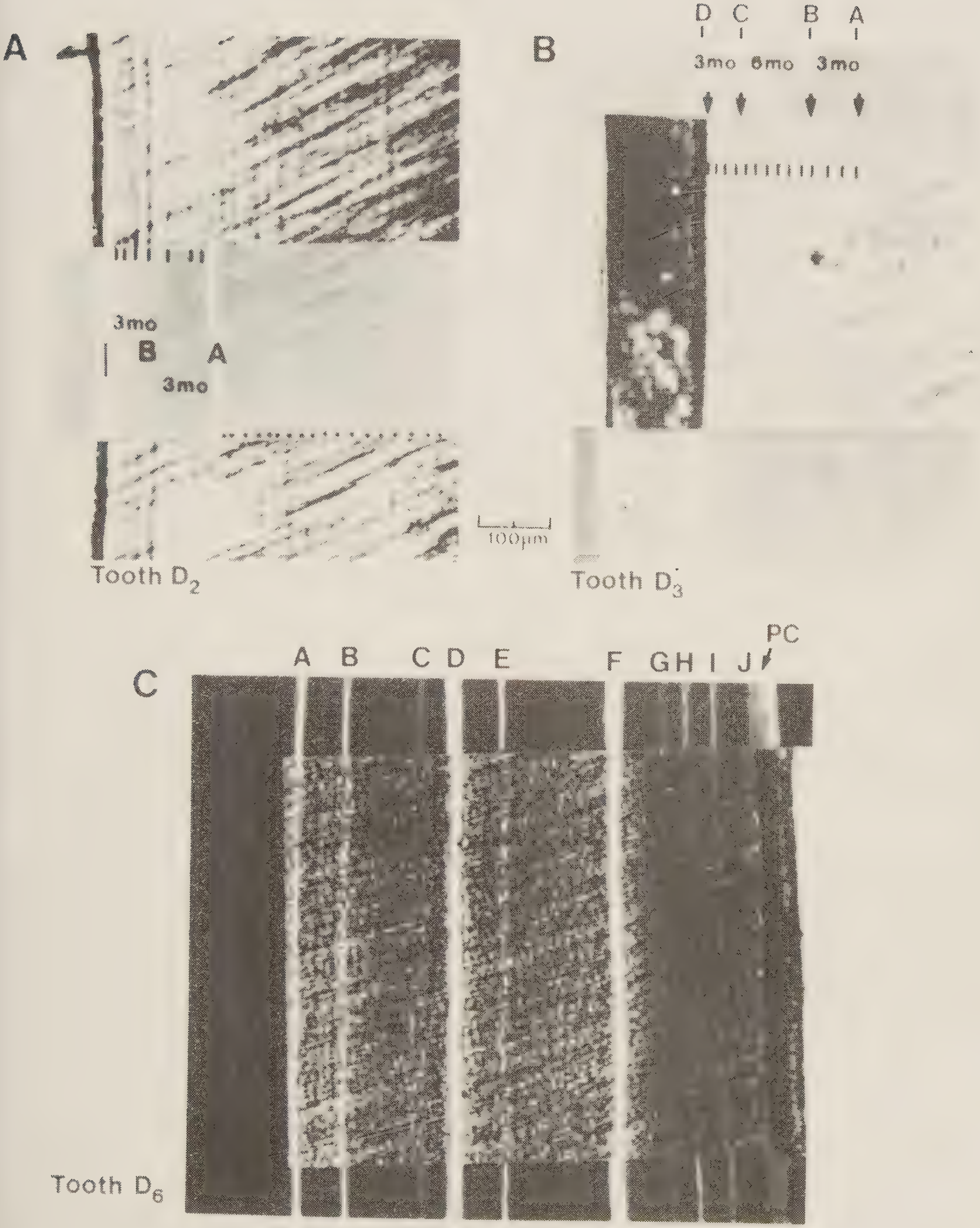

A
3mo
B
A
3mo
100μm
Tooth D_2
B
D
C
B
A
3mo
6mo
3mo
Tooth D_3
C
A
B
C
D
E
F
G
H
I
J
PC
Tooth D_6

Figure 7 Accumulation of labeled dentine in animal D. (A and B) UV micrograph swatches on light micrographs of dentine in second and third tooth extracted, respectively. The accumulating labels, dentine, and elapsed time are indicated. Drawn marks suggest numbers of fine layers between labels. (C) Swatch of light micrograph on UV micrograph of dentine in the last tooth extracted from animal D. (Original magnification, ×150.)

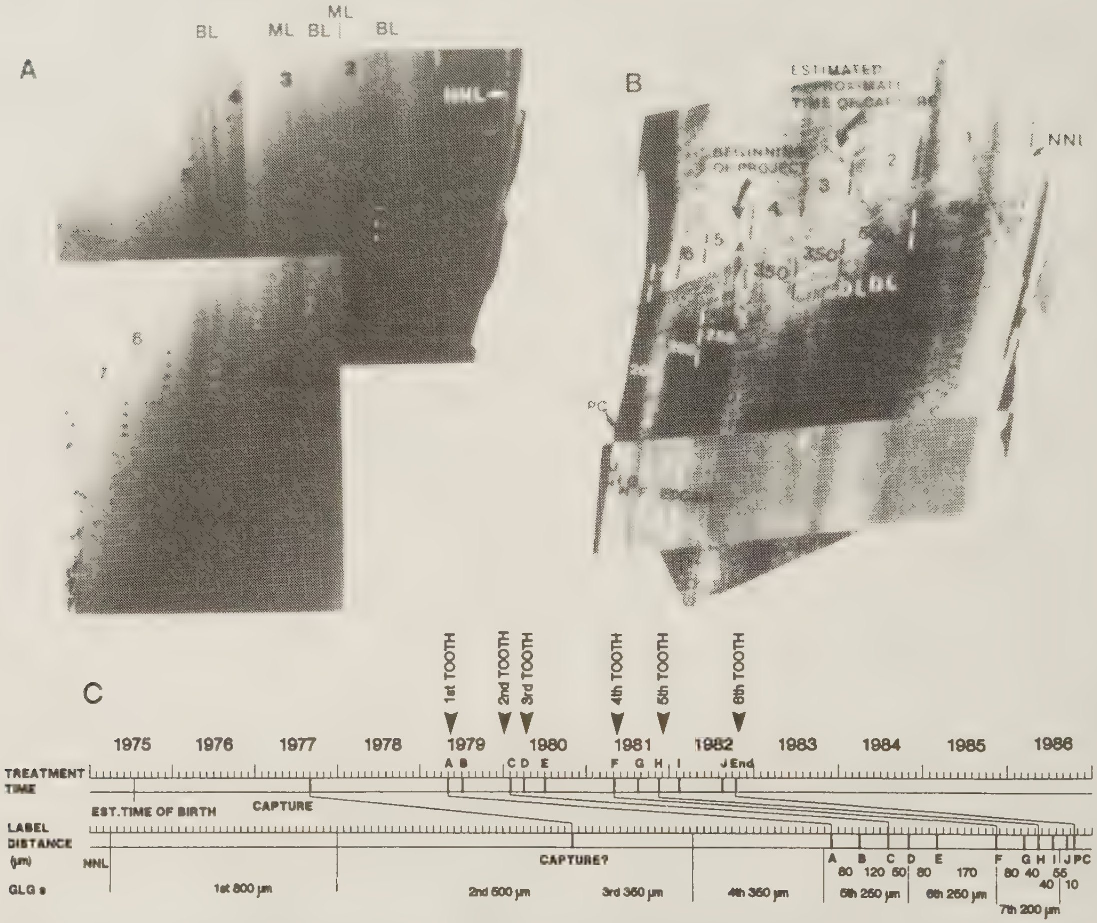

A
BL
ML
BL
ML
BL
NNL
1
2
3
4
6
7
B
ESTIMATED APPROXIMATE TIME OF CAPTURE
BEGINNING OF PROJECT
NNL
DLDL
350
350
250
PC
C
1st TOOTH
2nd TOOTH
3rd TOOTH
4th TOOTH
5th TOOTH
6th TOOTH
1975
1976
1977
1978
1979
1980
1981
1982
1983
1984
1985
1986
TREATMENT TIME
A B C D E F G H I J End
EST.TIME OF BIRTH
CAPTURE
LABEL DISTANCE (µm)
NNL
CAPTURE?
A B C D E F G H I J PC
80 120 50 80 170 80 40 55 40 10
GLG s
1st 800 µm
2nd 500 µm
3rd 350 µm
4th 350 µm
5th 250 µm
6th 250 µm
7th 200 µm

Figure 8 Calibration of GLGs in the last extracted tooth of animal D. (A) Decalcified and stained section showing GLG patterns featuring a single thin dark boundary layer (BL) (dotted lines) and a single thin dark mid-GLG (ML) layer. The boundary between the apparent fourth and apparent fifth GLG is indistinct due to the occurrence of several thin, dark-stained layers. (B) Untreated section with UV swatch showing labels (lettered). GLGs (bounded by dashed lines) are numbered and show thicknesses in micrometers. (C) Calibration chart showing birth and capture dates (estimated from capture body length and time in captivity) and annual GLG thicknesses based on estimated and monitored dentine deposition. (Original magnification of A and B, ×39. DLDL indicates dark–light–dark–light layer pattern in second GLG; GLG number one has a tripartite pattern; see Fig. 2 for other abbreviations.)

3.5-year project for eight of the twelve dolphins. Rates of deposition were computed for each animal by dividing thickness by the elapsed time in tenths of months. Because of age-specifc depositional patterns, younger individuals accumulated considerably more dentine per month than others. For this reason, and because of the possibility of population-specific thickness patterns, average monthly deposition by each animal during the monitored period was plotted on the same graph. The abscissa is scaled in 10-μm intervals, with absolute values omitted, and the period of the project, from spring 1979 to fall 1982, is represented on the ordinate with vertical lines set at successive January firsts (Fig. 9).

A common pattern in dentine depositional rates was discerned to some extent in all specimens: increased rates in spring and summer with de-

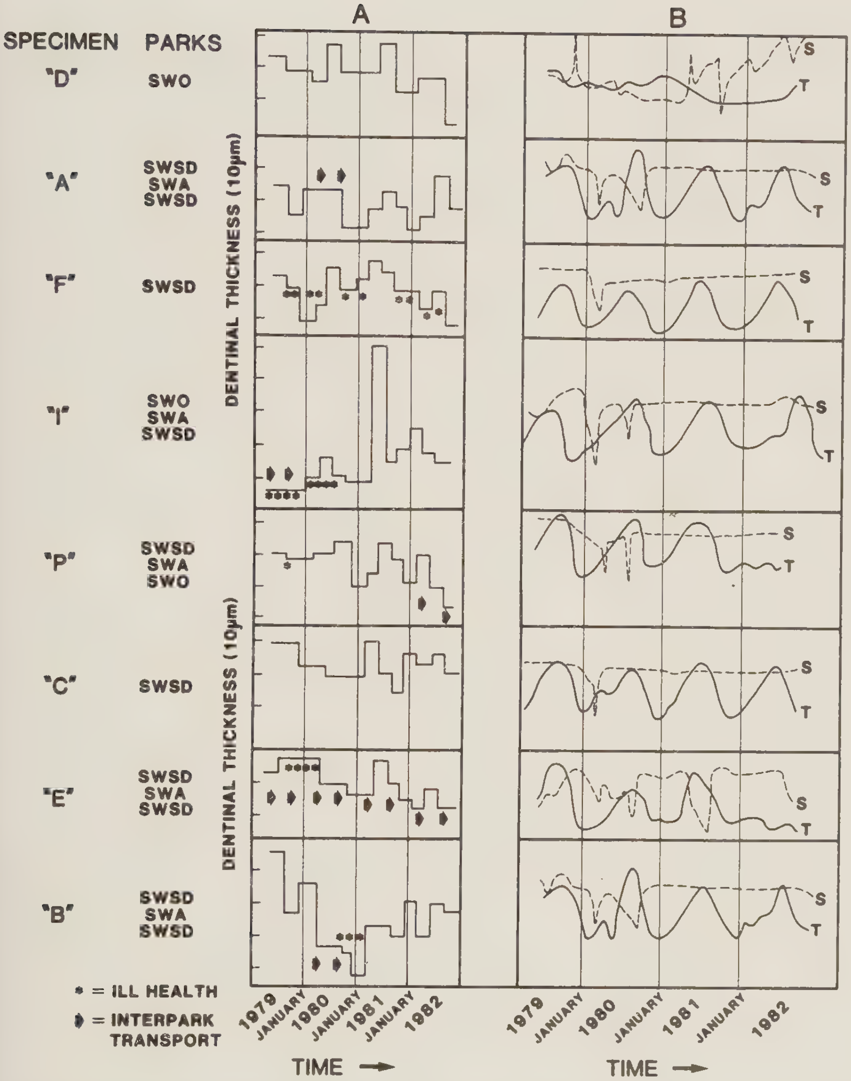


Figure 9 Monthly depositional rates and external environmental factors. (A) Relative average monthly rates of dentine deposition in eight bottlenose dolphins over a 3.5-year period, with plots of weekly measurements of water temperature (T) and salinity (S) (smoothed by eye) shown for each. (B) Vertical lines indicate January first of years shown. Rates tend to increase in individuals in spring–summer months and to drop in fall–winter months, although considerable wandering from this pattern is apparent. Depositional rate changes roughly correspond to but are not preceded by fluctuations in water temperature. They are not correlated with changes in salinity, nor with transport between Sea World parks (SWO, Florida; SWA, Ohio; SWSD, California). Arrows represent times of interpark transport, and asterisks indicate periods of ill health.

creased rates in fall and winter (Fig. 9A). This pattern, typified in plots for dolphins D and F, showed distinct and synchronized peaks and dips in mean rate over the entire 3.5-year period. The resemblance of relative changes in rates between these two animals was especially remarkable considering that D remained at SWO (Florida), where temperature and salinity are manipulated, and F remained at SWSD (California), where these two parameters are subject to ambient fluctuation.

Despite the striking similarities among many of the animals in depositional-rate cycles, however, there was noticeable variation in timing (e.g., B and E) and amplitude (e.g., I and P) within and between individuals. To test whether the spring–summer rate increase and fall–winter decrease amounted to a significant pattern, we compared synchronized drops and rises in rates among the eight animals for the 3.5-year period. For an animal, in each time segment (spring–summer or fall–winter) there can be only one of three possible outcomes: a peak matching a spring–summer segment, a drop matching a fall–winter segment, or something else that disrupts the ideal model of synchronized rate changes. If there is a common seasonal pattern that animals follow, there should be little difference in the frequency distribution of synchronized rate changes among animals.

A contingency table was set up with the rows representing animals and columns representing the three possible outcomes. Calculations gave a χ^2 value of 13.174 with $(8 - 1)(3 - 1) = 14$ df ($p = .5$). This indicates that the frequency distribution of the three outcomes is independent of the animals, and we conclude that the animals follow the synchronized cyclic model. Out of a potential 32 peaks and 32 dips in an ideal model of eight eight-season rate changes, the sample showed a 40% probability of peak (26 out of 64), a 40% probability of dip (again, 26 out of 64), and 12 out of 64 or a 20% probability of neither a synchronized dip nor peak.

Factors Possibly Affecting Dentinal Deposition

Exogenous Factors

The cyclic depositional rates of D illustrate how parameters were evaluated as possible influencing factors. Animal D had one of the most regular, cyclelike depositional patterns, yet experienced the most uniform environment. She was not transported between parks during the project, was never ill, and was not subjected to much or sudden fluctuation in water temperature (although water salinities temporarily fluctuated sharply several times). She usually ate no less than about 7.5–13 kg (20–35 pounds) of fish daily. She was not trained and did not participate in shows in the first year of the project. In the second year, training and show activity was frequent but did not affect her daily fish consumption; nor was it reflected by any noticeable difference in layering patterns or depositional rates in her teeth. In addition, D was kept at a lower latitude (Orlando, Florida) than any other animal in the project, yet she had one of the most distinctly cyclic changes in rate. This is contrary to what one might expect if day length were an important *zeitgeber* for changes in dentinal-deposition rates.

For all individuals, with the important exception of D, there were regular seasonal changes in water temperature which corresponded roughly with depositional rate changes in dentine, but none of the changes in water temperature or other physical parameters that we monitored consistently preceded changes in depositional rate (Figs. 9A, B). Thus, they do not seem to be causally related. In some cases, when water temperature had risen or had begun to rise, dentinal rate remained unchanged (e.g., P and C in 1980) or dropped (e.g., B and E in 1980). In other cases, when water temperature had started to decrease or had already reached a nadir, dentinal-deposition rate rose (e.g., E and B in winter 1979) or remained unchanged (e.g., C and E in winter 1980).

Perhaps more importantly, at various times depositional rates changed while water temperature (and other parameters) did not change. The rates of D in all years and of P and E from fall of 1981 to fall of 1982 followed a pattern of fall–winter decrease and spring–summer increase even though water temperature remained fairly constant. For D, mean water temperature was 16.4°C, with gradual changes between 13° and 20°C; for P and E water temperatures for 1982 fluctuated slowly between 14° and 18°C (Fig. 9B).

Changes in types of food given had no detectable effect on depositional rate. For example, A was fed fish of only one species in 1979, fish of mixed species in 1980, and fish and squid in 1981–1982. None of these changes were reflected in A's near-perfect cyclicity of winter decreases and summer increases in dentinal deposition.

Depositional rate changes and layering patterns typified by A, D, and F were unaffected by interpark transport. This is illustrated in A in 1980 and P in 1982. It is shown especially well in E. Dentinal accumulation for E was normal in 1981 and 1982 despite semiannual airplane transport of this dolphin (shown as arrows in Fig. 9A) between California and Ohio in all years during the project.

Endogenous Factors

A rare accident permitted us to examine possible effects of short-term stress in measurably altering layering patterns. A project animal leaped out of its tank and apparently was out of the water on the ground for hours before it was discovered. It was returned to its pool, presumably somewhat stressed. Using tetracycline labels to pinpoint the region of dentine formed at the time the dolphin was out of the tank, we were unable to detect any unusual lines or layers that might have reflected a physiological response to that incident.

Periods of sickness, however, did appear to affect depositional rate. The rate plot for F (Fig. 9A) is accompanied by several clusters of asterisks symbolizing bouts of sickness, usually indicated by inappetence. Distribution of these symbols corresponds with diminution of amplitude in changes of rate. For example, the drop in the rate in January 1980–1981, common in other dolphins plotted, is shallow in F, and the expected rise in spring–summer of 1982, common in most of the other animals, is equivocal in F. Conversely, the peaks in spring–summer 1980 and 1981, when F was not sick, are present in the plot. Similarly, P did not exhibit a decrease in depositional rate during fall–winter 1979, when he had a poor appetite and was receiving medication. However, his depositional pattern cycled normally during other years.

Animal E was not well during fall–winter of 1979. Beginning at about the same time, his dentinal-deposition rates departed from the presumed common pattern, which was not reestablished until winter 1980–1981. For I, symbols for interpark transport are concurrent with those of ill health in 1979, and the condition apparently was not normalized until mid 1980. During the period of sickness, there was very little change in the slow dentinal-deposition rate. The common pattern appeared in I in the spring of 1981 in what could be considered a compensatory acceleration of the rate. In fact, however, we have no data that provide a satisfactory explanation of this sudden escalation in rate. It is possible that this spurt in deposition represents variation in one tooth. It was documented in only the last tooth that was pulled.

For C, we have no data to account for either the lack of a peak in mid 1980 or an early increase in rate in winter of 1982. He remained in California during the entire period and was never ill or medicated. Salinity decreased sharply in early 1980 in C's tank, but similar sudden drops in salinity for other animals on various occasions (e.g., A in 1980 and E in 1981) did not result in disruptions of normal depositional cycles. If ill health was a factor in the apparent distortion of C's pattern, it was not detected by our observers.

Depositional rates of B differ markedly from those of A, although the two dolphins were subjected to almost identical conditions during the project (Fig. 9A, B). Part of this difference may be artifactual; the broad peak in the first half of 1980 for A is due in part to a mean rate computed using one measurement over 9 months during which no labels were introduced (Fig. 5A, C). However, comparisons of thicknesses of the second, third, and fourth GLGs for the two animals show that annual deposition was indeed less in B (Table 2). Animal B had a decreased appetite shortly before returning to San Diego from Ohio in 1980, and his record for the next 6 months is a picture of intermittently low food consumption accompanied by therapeutic treatments to help correct the condition (Figs. 5D and 9A). He was fully recovered by spring 1981, but his dentinal-deposition rate pattern remained largely unsynchronized relative to that exhibited in the other animals for the remaining 17 months of the study.

Cementum

Although cemental GLGs, each consisting of a light layer and a dark layer, were visible and countable, calibration of cementum was not possible in this study. The labels that we tried to introduce experimentally did not show up distinctly, apparently because our dosages of tetracycline were too weak for detection in cementum. We also were unable to match dentinal GLG counts with those of cementum using therapeutic labels. Often the cementum was too thin, or had fewer GLGs than the dentine, or showed the therapeutic labels in the wrong relative position. For example, in animal I the *XY* label, visible in about the third annual dentinal GLG (Fig. 3), was identified in about the eighth or ninth cemental GLG (Fig. 10). Cemental GLG counts, therefore, may be difficult to use as reliable indicators of age for this species.

CONCLUSIONS

Results of this long-term monitoring and marking study suggest that bottlenose dolphins deposit a specific annual thickness of dentine at a given age in a predetermined pattern which is largely under endogenous control. In healthy animals of our sample, the pattern of GLG deposition was generally unaffected by conditions of captivity, including changes in water temperature or salinity, physical activity, at least some kinds of short-term stress, type of food consumed, and possibly even differences in latitude.

Rates of dentinal deposition were fairly cyclic, tending to increase in the spring and summer and to decrease in the fall and winter. They seem to have altered somewhat when the animals were ill and for some period after the illnesses. Apparently, they were not strongly entrained by any external *zeitgeber* that we were able to detect. However, the following observations suggest that some entrainment cue or complex of cues exists: (1) there was a rough correspondence of depositional rate changes with regular changes in water temperature, with a number of important exceptions, (2) to some extent rate peak and depression varied in time and in amplitude in an animal and

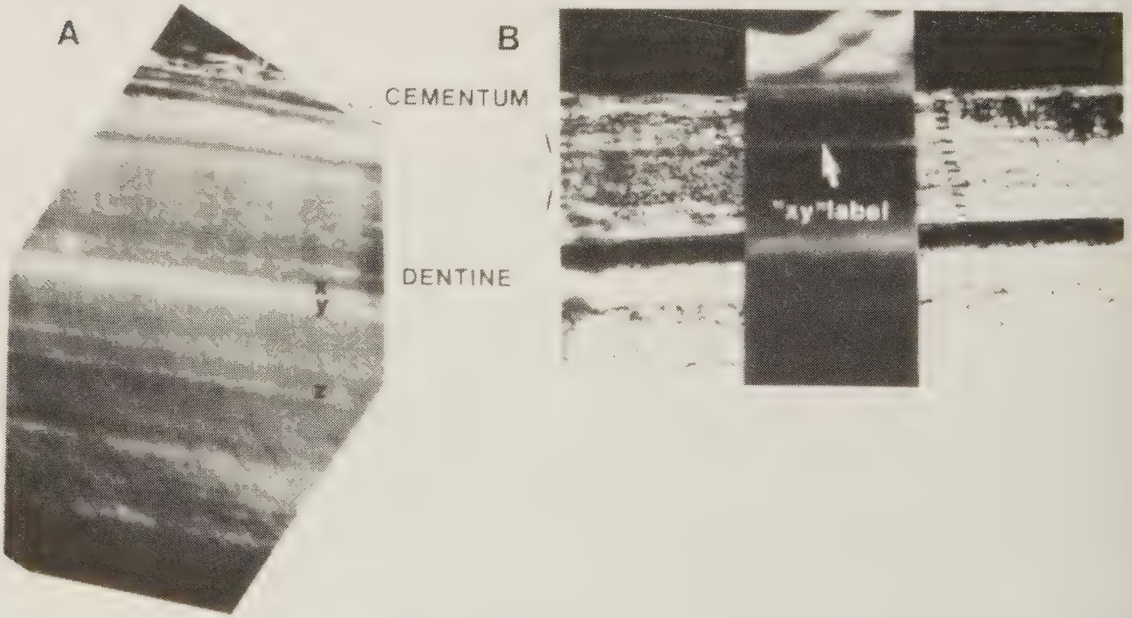


Figure 10 Unreliability of cemental layers for estimating age. (A) UV micrograph of area of tooth tissue including cementum from animal I (more detail and calibration are shown in Fig. 3). Preproject labels *X* and *Y* were presumably introduced at or near capture, when I was only a few years old. The labels occur in approximately the third dentinal GLG (×39). (B) Light micrograph of cementum from I with swatch of UV micrograph showing what is interpreted to be the *XY* label in approximately the eighth or ninth cemental GLG (×150). This example suggests that cemental GLG deposition is not necessarily correlated with that of dentine.

between animals, and (3) in some specimens, after being unsynchronized for a time, deposition cycles usually became resynchronized. The *zeitgeber* was not identified in this study.

Although the sample from the California coast consisted of only two animals including one captive-born hybrid, comparisons with the sample from Florida suggest that the age-specific annual thickness of dentine may be manifested as two population-specific patterns: one for Atlantic animals and one for Pacific animals. Studies using labels in additional captive animals from the Pacific should help to decide this question.

In untreated thin sections viewed in plain light, the annual GLG consists of two light layers each followed by a darker layer. In decalcified and stained thin sections, in plain transmitted light, each annual GLG tends to have one or more dark-stained layers near its boundary and one or more near its midpoint. The dark-stained mid-GLG layer(s) bisects the otherwise lightly stained GLG. All GLGs tend to be bipartite except the first GLG formed, which tends to be tripartite. Fine layers within the GLGs are probably formed monthly.

We were not able to calibrate cemental layers with dentinal layers in this study. Tetracycline labels could not be used to match GLGs in dentine and cementum. This suggests that cemental layers may have no simple relationship to annual GLGs deposited in dentine. In our opinion, cemental GLGs alone should not be relied on for estimating ages of bottlenose dolphins.

A tetracycline label immediately internal to the neonatal line in one captive-born animal was coincident with tetracycline treatment of its mother. This supports the suggestion by Myrick *et al.* (1984) that it may be possible to treat nursing calves in ill health with certain drugs that combine with constituents of milk by medicating the lactating mothers. The label's closeness to the neonatal line is also corroborating evidence that the neonatal line forms at or near the time of birth.

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REFERENCES

Best, P. B. (1976). Tetracycline marking and the rate of growth layer formation in the teeth of a dolphin (*Lagenorhynchus obscurus*). *S. Afr. J. Sci.* **72,** 216–218.

Gurevich, V. S., Stewart, B. S., and Cornell, L. H. (1981). The use of tetracycline in age determination of common dolphins, *Delphinus delphis*. *In* "Age Determination of Toothed Whales and Sirenians"(W. F. Perrin and A. C. Myrick, Jr., eds.), pp. 165–169. *Rep. int. Whal. Commn*, Spec. Issue 3.

Hui, C. A. (1978). Reliability of using dentin layers for age determination in *Tursiops truncatus*. U.S. Marine Mammal Comm. Rep. No. MMC-77/09 (Natl. Tech. Info. Serv. PB288444). 25 pp.

Kasuya, T. (1977). Age determination and growth of Baird's beaked whale with a comment on the fetal growth rate. *Sci. Rep. Whales Res. Inst., Tokyo* **29,** 1–30.

Laws, R. M., (1962). Age determination of pinnipeds with special reference to growth layers in the teeth. *Saugetier. Mitt.* **27**(3), 129–146.

Myrick, A. C., Jr. (1979). Variation, taphonomy, and adaptation of the Rhabdosteidae (=Eurhinodelphidae) (Odontoceti, Mammalia) from the Calvert Formation of Maryland and Virginia. Ph.D. thesis, Univ. of California, Los Angeles. 411 pp. (Unpublished.)

Myrick, A. C., Jr. (1981a). Some approaches to calibration of age in odontocetes using layered hard tissues. *In* "Age Determination of Toothed Whales and Sirenians"(W. F. Perrin and A. C. Myrick, Jr., eds.), pp. 95–97. *Rep. int. Whal. Commn*, Spec. Issue 3.

Myrick, A. C., Jr., (1981b). Examination of layered tissues of odontocetes for age determination using polarized light microscopy. *In* "Age Determination of Toothed Whales and Sirenians" W. F. Perrin and A. C. Myrick, Jr., eds.), pp. 105–112. *Rep. int. Whal. Commn*, Spec. Issue 3.

Myrick, A. C., Jr., Hohn, A. A., Sloan, P. A., Kimura, M., and Stanley, D. D. (1983). Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. NOAA-TM-NMFS-SWFC-30. 17 pp.

Myrick, A. C., Jr., Shallenberger, E. W., Kang, I., and MacKay, D. B. (1984). Calibration of dental layers in seven captive Hawaiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. *Fish. Bull. (U.S.)* **82**(1), 207–225.

Nielsen, H. G. (1972). Age determination of the harbour porpoise *Phocoena phocoena* (L.) (Cetacea). *Vidensk. Medd. Dan. Naturhist. Foren.* **135,** 61–84.

Nishiwaki, M., and Yagi, T. (1953). On the age and the growth of teeth in a dolphin, (*Prodelphinus caeruleoalbus*). (I). *Sci. Rep. Whales Res. Inst., Tokyo* **8,** 133–146.

Perrin, W. F., and Myrick, A. C., Jr., eds. (1981). "Age Determination of Toothed Whales and Sirenians." *Rep. int. Whal. Commn,* Spec. Issue 3. 229 pp.

Ridgway, S. H., Green, R. F., and Sweeny, J. C. (1975). Mandibular anesthesia and tooth extraction in the bottlenose dolphin. *J. Wildl. Dis.* **11,** 415–418.

Scheffer, V. B., and Myrick, A. C., Jr., (1981). A review of studies to 1970 of growth layers in the teeth of marine mammals. *In* "Age determination of Toothed Whales and Sirenians" (W. F. Perrin and A. C. Myrick, Jr., eds.), pp. 51–63. *Rep. int. Whal. Commn,* Spec. Issue 3.

Sergeant, D. E. (1959). Age determination in odontocete whales from dentinal growth layers. *Nor. Hvalfangst-tidende* **48,** 273–288.

Sergeant, D. E., Caldwell, D. K., and Caldwell, M. C. (1973). Age, growth, and maturity of bottlenosed dolphins *(Tursiops truncatus)* from northeast Florida. *J. Fish. Res. Board Can.* **30,** 1009-1011.

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POPULATION REGULATION, CONVERGENCE, AND CANNIBALISM IN *NOTONECTA* (HEMIPTERA)[1]

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Abstract. In a population convergence experiment, the initial densities of adults of the predatory backswimming bug *Notonecta hoffmanni* were set above and below a putative equilibrium density in stock tanks. The experiment was done at two constant rates of food supply (wingless *Drosophila*) for the larger instars (in natural pools *Notonecta* feed mainly on terrestrial arthropods that fall on the water surface). It was predicted that the densities of the resulting populations would converge on an equilibrium set by the rate of food supply for the larger instars. The tanks also contained zooplankton (mainly *Daphnia*), which were the main food supply of the smaller instars of *Notonecta*. The resulting overwintering populations converged towards the appropriate equilibrium densities, via density-dependent and food-dependent fecundity and then cannibalism. However, the populations overshot their equilibria, producing overconvergence. In natural populations such overconvergence might tend to produce 2-yr cycles in abundance. Overconvergence resulted from the insensitivity of the survivorship of the original adults (at least over the short term) to differences in food supply between treatments, allowing them to continue to affect (via cannibalism and reproduction) the eventual density of the new overwintering population. Because *Notonecta* population density was determined by the externally supplied, locally uncoupled food supply, even though the early instars depended for food largely upon dynamic populations of zooplankton, the dynamics of the *Notonecta* population were simpler than a description of the food web might suggest.

Key words: backswimming bug; cannibalism; convergence; cycle; experimental ecology; freshwater; Notonecta; *population dynamics; predation.*

INTRODUCTION

Interactions among populations in communities containing true predators are potentially very complex. The complexity has several sources. First, true predators typically are polyphagous and thus link the dynamics of a number of prey species. Second, and especially in freshwater communities, the size and species of prey in the predator's diet typically change as it grows (e.g., Werner and Gilliam 1984, Bence and Murdoch 1986, Murdoch and Bence 1987). Third, true predators are often cannibalistic, raising the potential for complex internal size- and age-dependent dynamic interactions whose intensity in turn is influenced by the density of a variety of prey species (Fox 1975*a*, Polis 1981). Although much progress has been made in the last decade in modelling interactions between age-distributed populations (e.g., Hastings 1984, Murdoch et al. 1987), these complexities nevertheless pose a daunting challenge to developing useful models involving true predators.

This paper examines some aspects of the dynamics of age-structured polyphagous predators that might render their analysis simpler than the predator's complex food web suggests is possible. Our predator is the backswimming freshwater bug, *Notonecta,* which is in many ways an archetypal freshwater predator. *Notonecta* lives all of its life in freshwater, passing through six instars and a large size range. It is highly polyphagous, and its diet changes with size. Older, larger instars cannibalize younger, smaller instars at a rate influenced by their food supply (Fox 1975*c*). Its generation time is typically longer than those of its prey species, sometimes by as much as an order of magnitude. The delays implicit in *Notonecta*'s age distribution are thus likely to be important dynamically (Murdoch and Bence 1987).

Some features of *Notonecta* make it especially suitable for our purposes. First, we know that *Notonecta* are food limited in their natural stream environment in southern California: they have one generation per year and their density is strongly influenced by the food supply of the reproductive adults (Fox 1975*b, c*). Second, extensive studies have been done in our laboratory on *Notonecta*'s predatory behavior (Fox 1973, Scott 1980, Chesson 1981, 1989, Scott and Murdoch 1983), and on the effects of food supply on its development (Fox and Murdoch 1978, Scott 1980), and we have been able to show that these laboratory studies provide an adequate basis for predicting *Notonecta*'s effects upon the population dynamics of its prey species (Murdoch and Scott 1984, Murdoch et al. 1984). Finally, in nature the larger instars eat mainly terrestrial prey items (insects, etc.) that fall on the surface of the water (Fox 1975*b*), and laboratory studies suggest that larger instars prefer such items to resident planktonic prey (Chesson 1981). This suggests (and we confirm in this paper) that the dynamics of the food supply of the larger instars, and especially of the adults, are uncoupled both from other prey species and from the *Notonecta* themselves, even when the small instars can feed on a complex planktonic fauna.

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In our experiments we posed several questions, trying in each case to exploit this decoupling of dynamics to clarify how the various components in the system interact and to determine whether some components can be ignored for certain purposes. We present the results of a "convergence" experiment, in which initial *Notonecta* density is manipulated above and below a putative equilibrium density, and evidence is then sought that the population returns to equilibrium. Those treatments are crossed with the manipulation of the putative equilibrium, which is determined by the food supply for large instars. We ask whether a distinct food supply for large instars, and cannibalism, together suppress the importance of small-instar dynamics (in particular their interactions with their planktonic food supply) in determining the final density of the overwintering *Notonecta* population.

METHODS

Laboratory experiments

Experiments were done at 25°C with a 12L:12D light regime. All *Notonecta* and prey were from stock laboratory cultures. With the exception of *Drosophila* all cultures were originally derived from stock tanks in the Santa Ynez Valley in southern California. Experiments were done in 500-mL plastic tubs.

Preference experiments.—Two prey species were offered in initially equal numbers (20 of each species), and were not replaced during each 2-h trial. Before an experiment each *Notonecta* was fed excess mosquito larvae for 24 h, and then starved for 24 h. There was zero mortality in controls without predators. Large *Daphnia* (mean [±SD] length 2.05 ± 0.18 mm), large *Ceriodaphnia* (length 0.78 ± 0.04 mm), adult *Drosophila* (length 2.28 ± 0.21 mm), and instar I *Notonecta* (length 2.81 ± 0.14 mm) were the prey. One experiment measured *Notonecta*'s preference between *Drosophila* and *Daphnia*, and between *Drosophila* and *Ceriodaphnia*. A second experiment measured *Notonecta*'s preference between instar I *Notonecta* and each of these three prey species.

Preference was measured by

$$\alpha_i = \ln(R_i/N_i)/\sum_{j=1}^{k} \ln(R_j/N_j) \tag{1}$$

where N_i and R_i are number of prey of species i present initially and at the end of the experiment, respectively, k is the number of species, and α_i varies from 0 to 1 (Chesson 1983). When there is no preference $\alpha_i = 1/k$ (i.e., $\alpha_i = 0.5$ in the two-species case).

Feeding rate.—All individuals were starved for 24 h; then for 24 h before the experiment one set of *Notonecta* ("starved") was starved while the second set ("well-fed") was fed excess mosquito larvae. Fifty *Drosophila* were added at the start of the experiment, which ran for 2 h. Prey were not replaced.

The "high" *Drosophila* treatments at the start of the stock tank experiment were given enough *Drosophila* to allocate to each adult *Notonecta* approximately the number of flies eaten per day by well-fed adult notonectids in this laboratory experiment.

Cannibalism rate.—We counted the number of instar I *Notonecta* eaten by instar IV and (young) adults over 24 h in the presence of various combinations of alternative prey. All treatments contained *Ceriodaphnia* and *Notonecta* instar I. The *Ceriodaphnia* served as food for the instar I to prevent them from dying of starvation during the experiment, and has negligible effects on cannibalism by large *Notonecta* (Scott 1980, see also Table 2). We examined cannibalism rate on instar I *Notonecta* when only instar I and *Ceriodaphnia* were present as prey and when, in addition, either *Daphnia* or *Drosophila* were provided as alternative prey for the large *Notonecta*. For 24 h before the experiment, cannibals and instar I nymphs were fed excess amounts of the alternative prey that they would encounter during the experiment.

During the first 12 h of the 24-h experimental period an excess (≈500) of *Ceriodaphnia* was maintained in all treatments. Alternative prey for adults were given far in excess of the feeding rate (250 *Daphnia* or 125 *Drosophila* initially, with smaller batches added every 2 h to replace prey that were eaten). Two large *Notonecta* and 10 instar I were added to each tub initially. Notonectids were censused every hour for the first 12 h, and then again at 24 h. Dead instar I and those that molted to instar II were removed and replaced.

Stock tank experiments

Outdoor galvanized steel stock tanks (1.8 × 0.6 × 0.6 m) lined with fiberglass were filled to a depth of 0.5 m with 500 L deionized tap water in March 1981, with water lost to evaporation replaced weekly thereafter. Beginning in March inocula of algae (mainly *Chlamydomonas* and *Chlorella*) and the local community of zooplankton (*Daphnia, Ceriodaphnia,* ostracods, and some rarer species) were added over 4 mo and allowed to grow. Before the experiment, in early July, 20 (of 25) tanks with the most similar communities of algae and zooplankton were selected, and their contents mixed (among tanks) to reduce initial variability. Eight of these 20 tanks were selected, randomly, for use in the experiment described here.

Each tank was covered with fiberglass screening after it was first filled in March. Tanks were inspected several times a week and extraneous predators (mainly odonate naiads and beetle larvae) were removed.

The experiment lasted 90 d. At the start of the experiment (on 16 July) each tank was stirred and then divided in half by a resin-coated plywood barrier placed perpendicular to the long sides. Rubber fittings around the edge of the plywood prevented movement of zooplankton between the two sides. *Notonecta* were then added.

Most *Notonecta hoffmanni* in southern California overwinter as adults. The entire life cycle (egg, five nymphal instars, adult) is spent in the water, and adults rarely fly. Reproduction begins in early spring and may continue through early fall if food supply and temperatures are favorable (Fox 1973, Scott 1980). Under favorable conditions (25°, and excess food) eggs hatch in 15 d, development from first instar to adult may occur in <45 d, but development rate is temperature and food dependent (Fox 1973, Fox and Murdoch 1978).

Experimental design

In a 2 × 2 factorial experiment ($n = 4$ per treatment), two food treatments, high (200 *Drosophila*/d) and low (50 *Drosophila*/d) were assigned among the eight tanks at random, and were crossed with two initial *Notonecta* density treatments, low (two pairs of adults) and high (eight pairs of adults), assigned at random to the two sides of each tank. (The same number of first instars were also added, but virtually all were cannibalized and we do not discuss these inocula further.) A given tank thus had the same number of *Drosophila* on both sides, but low *Notonecta* density on one side, and high on the other. The initial *Notonecta* densities were well within the range of natural densities in local stock tanks and stream pools. *Drosophila* were added daily inside floating cages that constrained them to the water surface, after those remaining from the previous day had been removed. Each cage had styrofoam sides made from the bottom half of an egg carton, no floor (allowing *Notonecta* access to the *Drosophila*), and a roof of 0.25-mm Nitex screening.

Daily mean water temperature was relatively constant during the first two-thirds of the experiment (21°–26°), but dropped into the 16°–21° range by day 70. Daily fluctuations in water temperature were typically in the range of 6°–8°, while variation between tanks was 1°–2°.

Notonecta were censused every 3–4 d. First, all visible *Notonecta* were counted. We then netted *Notonecta* into buckets of water, instars I and II being kept separately. Netting then continued until five consecutive sweeps yielded no additional *Notonecta* or exuviae. If the visual count or the previous census indicated there were still individuals not accounted for, the census procedure was repeated. Individuals were then classified by instar and sex (adults only), and returned to the tank. Dead adults were also sexed, and classified as old or new generation based on the condition and coloration of the hemelytra. The number of hatched and unhatched eggs present on buoyed removable strips of black plastic Vexar was counted. Vexar is a preferred substrate for egg laying by *Notonecta* (L. R. Fox 1970 and *personal observation*). Some eggs were laid on the sides of the tank and were not counted.

After *Notonecta* and Vexar strips were removed, the water was stirred to mix the contents evenly. Zooplankton densities were then sampled by placing a 500-mL jar halfway down the water column, inverting the jar, and placing the contents in a bucket. This was done nine times on each tank side, the samples being evenly spaced on a 3 × 3 sampling grid. A 500-mL subsample of the water in the bucket was taken, filtered through 153-μm mesh, and preserved in 95% ethanol. The water and animals remaining in each bucket were then poured back into the tank. This procedure was repeated and a second sample was preserved.

Daphnia was almost the sole zooplankter eaten by *Notonecta* and at the start of the experiment there were no significant differences in *Daphnia* density among treatments (ANOVA F tests, all $P > .1$). The *Daphnia* population on both sides of one tank crashed to extinction by day 8, and never reappeared; this tank is excluded from all analyses. Considering all other experimental tanks there were no significant differences in mean *Daphnia* density between treatments during (the mean over the entire experiment) or at the end of the experiment (ANOVA F tests, all $P > .1$).

Observations on feeding of *Notonecta* were made during 10-min periods at various times throughout the experiment. Records were made, by instar, of the number of *Notonecta* feeding, and the prey type they were consuming.

Calculation of Notonecta *vital rates*

For each instar, i, during each intercensus period, $t - 1$ to t, we wish to estimate the number recruiting (molting) into the instar, $M_{i,t}$, the number dying, $D_{i,t}$, and egg production, E_t. The relevant numbers collected at each census are the number alive in each instar, $N_{i,t}$, the number of corpses, $C_{i,t}$, the number of exuviae (cast skins), $S_{i,t}$, and the number of new and hatched eggs. (Note that we denote census date for numbers observed at a census, or numbers recruited or lost between two censuses, with a lower case t.)

To reduce errors we make use of cumulative counts in our estimates. Cumulative totals of the number of corpses, $C_{i,T}$, and exuviae, $S_{i,T}$, in each instar, and of the number of unhatched and hatched eggs were either directly observed or calculated as simple sums. For each census we also estimated the cumulative number ever recruited to the instar, $M_{i,T}$, and the cumulative number ever to have died in the instar, $D_{i,T}$. (To contrast these cumulative counts with the numbers actually counted or estimated at each census [previous paragraph] we replace t by T as the subscript referring

TABLE 1. Preference of *Notonecta* between *Drosophila* and *Daphnia*. The values given are the mean number of prey of each type eaten during 2-h trials and the mean preference for *Drosophila* (α_{dros}), both ±1 SE. (Instar I trials were run for 6 h to obtain adequate numbers eaten.)

	Number of prey eaten		Preference†		
Instar	Alternative prey (*Daphnia*)	*Drosophila*	α_{dros}	t	(df,)
I	6.1 ± 1.4	1.7 ± 0.2	0.2 ± 0.06	3.83**	(9)
II	9.6 ± 0.5	1.0 ± 0.2	0.08 ± 0.02	21.00***	(9)
III	14.8 ± 1.7	2.3 ± 0.4	0.11 ± 0.05	7.80***	(7)
IV	9.6 ± 0.9	4.4 ± 0.7	0.28 ± 0.05	4.40**	(9)
V	5.7 ± 2.1	9.1 ± 2.0	0.64 ± 0.11	1.27	(7)
Adult	1.7 ± 0.4	7.6 ± 2.0	0.74 ± 0.10	2.40*	(9)
	Alternative prey (*Ceriodaphnia*)	*Drosophila*			
II	3.3 ± 0.9	2.2 ± 0.3	0.55 ± 0.12	0.42	(9)
IV	0.4 ± 0.2	8.3 ± 0.03	0.94 ± 0.03	14.67***	(9)
Adult	0.6 ± 0.2	5.2 ± 1.6	0.82 ± 0.08	4.00**	(9)

† Significant deviations from random selection ($\alpha_{dros} = 0.5$) were tested by t tests. There were 8–10 replicate trials for each instar.

* $.01 < P < .05$; ** $.001 < P < .01$; *** $P < .001$.

to census date.) The number entering into an instar or dying within an instar within a census period is then obtained simply by subtracting the cumulative number at census $t - 1$ from that at census t. Over the entire experiment only a few individuals that were counted as instar I could not be accounted for, either as eventual survivors or as corpses. Nor did our censuses of later stages ever exceed the number expected from counted recruits to earlier stages. Thus all stages (except eggs) were counted with virtually no error.

The cumulative number of exuviae of the preceding instar gives a minimum estimate of the number ever recruited into an instar by time t, $M_{i,T}$. However, this may be an underestimate, especially for the smallest instar. We therefore first calculate $M_{i,T}$ for the largest instar, the adults. This is simply the number present at time t plus the cumulative number of adult corpses found up to time t, with the constraint that the cumulative number can never decrease, and if it does, the number from the previous census is retained. Each adult typically was counted many times in its life, and there was never an inconsistency in the estimates of the number recruiting to the adult stage based on fifth-instar exuviae vs. direct counts of adults.

$M_{i,T}$ was then calculated for progressively smaller instars by noting that the estimated cumulative number recruited to the instar is the sum of the number alive in the instar at time t ($N_{i,t}$), plus the number that ever recruited out of it ($M_{i+1,T}$) plus the number that ever died in the instar ($D_{i,T}$):

$$M_{i,T} = N_{i,t} + D_{i,T} + M_{i+1,T}. \qquad (2)$$

$N_{i,t}$ is again known without error, and $M_{i+1,T}$ has just been calculated. A minimum estimate of $D_{i,T}$ is provided by the cumulative number of corpses, and again the only source of error is current corpses that have not been found. A further check is now possible, since $M_{i,T}$ calculated in this way should not be smaller than its estimate based on the cumulative numbers of exuviae and corpses, and should not decline through time. For instars II and older, only 1 or 2% of estimates ever presented such inconsistencies, and these concerned only one or two individuals. In these cases, Eq. 2 was balanced by increasing the estimated number of cumulative deaths in the instar.

Inconsistencies were more common in instar I, due mainly to delayed recovery of corpses and exuviae. A second, minimum, estimate of recruitment to instar I was provided by the cumulative number of hatched eggs. On the occasions that the egg count gave a higher estimate than Eq. 2, the egg count was used.

TABLE 2. Number of each prey type ($\bar{X}$ ±1 SE) eaten in 2 h (E_A = number of alternative prey eaten, E_I = number of instar I eaten) and mean preference (α_I) for instar I by large *Notonecta* given a choice between 10 instar I nymphs and 30 individuals of an alternative prey type.

Predator	Alternative prey	N	E_I	E_A	α_I	t
Instar IV	*Drosophila*	6	1.7 ± 0.6	14.5 ± 2.9	0.26 ± 0.08	2.1†
Adult	*Drosophila*	6	0.3 ± 0.2	6.7 ± 1.5	0.12 ± 0.08	4.75**
Adult	*Daphnia*	6	1.7 ± 0.2	13.5 ± 3.0	0.28 ± 0.09	7.5***
Adult	*Ceriodaphnia*	5	1.6 ± 0.4	0	1.00	...

† $.05 < P < .10$; ** $.001 < P < .01$; *** $P < .001$.

RESULTS

Preference and cannibalism rates

Laboratory experiments measured *Notonecta*'s preferences among the major prey species present in the stock tanks, and also measured the effect of these prey on cannibalism by large upon small *Notonecta*. These experiments were designed to improve our interpretation of cannibalism in the stock tanks. *Drosophila, Daphnia,* and *Ceriodaphnia* were the three prey types available in the tanks.

The early instars of *Notonecta* strongly preferred *Daphnia* over the larger *Drosophila,* but preference for *Drosophila* increased with *Notonecta* size, the changeover occurring in instar V (Table 1). All three instars we tested (II, IV, adult) preferred *Drosophila* to *Ceriodaphnia,* which is much smaller than *Daphnia*; the preference was strong in the larger two instars, but not statistically significant for instar II. These results are consistent with other research indicating that prey size relative to predator size is a key variable determining preference by *Notonecta* (Scott and Murdoch 1983).

These results, combined with those of Chesson (1981) and Scott and Murdoch (1983), show that, among the three species given, *Daphnia* is the preferred prey for instars I–IV, that instar V tends to prefer *Drosophila* (but not significantly),while adults prefer *Drosophila. Ceriodaphnia* is the least preferred by all stages of *Notonecta,* with preference for *Ceriodaphnia* decreasing with size of the predator.

A reasonable expectation is that the preference of adult notonectids for smaller conspecifics should be highest when *Ceriodaphnia* is the only other prey available, and lowest when *Drosophila* is present. This prediction was confirmed in a laboratory experiment (Table 2). Preference of adult *Notonecta* for first-instar *Notonecta* was lowest when *Drosophila* were present, intermediate when *Daphnia* were present, and highest when *Ceriodaphnia* was the alternative prey. Instar-IV nymphs were tested only with *Drosophila* as the alternative prey and preferred *Drosophila* to instar-I notonectids.

Two factors in addition to preference will influence the cannibalism rate in the presence of alternative prey. First, hunger strongly affected the number of prey eaten: starved adult *Notonecta* presented only with *Drosophila* ate more than twice as many of this prey per day ($\bar{X} \pm \text{SE} = 31.7 \pm 4.2$ prey/d, $N = 6$) as did well-fed adults (13.4 ± 3.7 prey/d, $N = 10$), *t* test, $P < .01$. Second, larger preferred prey lowered the attack rate on the alternative prey more than would have been predicted on the basis of preference alone, because handling time is longer (Chesson 1989). The effects of these two factors are apparent in the next set of results.

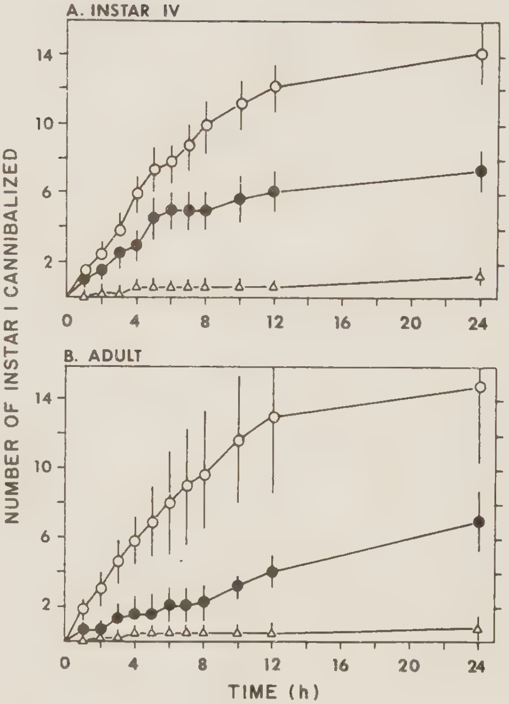

FIG. 1. Cumulative numbers of instar I eaten over a 24-h period (means ± 1 SE) by (A) instar IV and (B) adult *Notonecta.* Alternative prey were *Ceriodaphnia* alone (○), *Ceriodaphnia* plus *Daphnia* (●), and *Ceriodaphnia* plus *Drosophila* (△).

Cannibalism rates of *Notonecta* instars IV and young adults upon *Notonecta* instar I were measured over 24 h: (1) in the presence of *Ceriodaphnia* alone, (2) with *Ceriodaphnia* plus *Daphnia,* and (3) with *Ceriodaphnia* plus *Drosophila.* (*Ceriodaphnia* was provided as food for instar I and had almost no effect on cannibalism, see Methods). The results are as expected (Fig. 1); alternative prey (*Daphnia* and *Drosophila*) significantly reduced the number of instar I cannibalized in 24 h by both adults and instar IV (two-way ANOVA, main effect of alternative prey: $F_{2,18} = 21.05$, $P < .001$). The cannibalism rate of adults was lowest in the presence of *Drosophila,* which was more preferred by adult *Notonecta* and required a longer handling time (4.8 min) than *Daphnia* (1.5 min). Cannibalism by instar IV was also more suppressed by *Drosophila* than by *Daphnia,* even though the latter was preferred (Table 1). The reason appears to be that handling time of instar IV is six times as long on *Drosophila* (12 min) as on *Daphnia* (2 min), and the former presumably also lowers hunger more than *Daphnia* does. There was no difference in the number of instar I eaten by adults vs. instar IV (two-way ANOVA, main effect of *Notonecta* stage: $P > .1$).

Observations made during the stock tank experiment showed that diets in the field followed the pattern of preferences established in the laboratory (Table 3). *Daphnia* was the major item in the diets of early *Notonecta* instars but was rarely eaten by larger instars,

Table 3. Percentage of observed *Notonecta* meals in stock tanks composed of each prey type. *N* is the number of feeding observations. "Other" includes miscellaneous prey such as chironomids and corixids.

	Prey type					
Predator	*Drosophila*	Cladocera*	Ostracoda	*Notonecta*	Other	*N*
Instar I	5.4	78.3	9.8	1.1	5.4	992
Instar II	2.4	86.3	4.2	2.4	4.8	168
Instar III	11.7	59.2	0.8	18.3	10.0	120
Instar IV	23.3	23.3	3.3	26.7	23.3	30
Instar V	44.1	2.9	0	41.2	11.8	34
Adult	50.0	2.3	0	29.6	18.2	44

* Nearly all of the Cladocera eaten were *Daphnia,* but in a few cases when smaller Cladocera were being consumed we could not determine whether these were *Ceriodaphnia* or *Daphnia.*

while the opposite was true of *Drosophila.* The three smaller *Notonecta* were the main predators of *Daphnia,* while large predators were the main cannibals of young *Notonecta. Ceriodaphnia* were rarely eaten.

These results from the tanks can be used only to confirm the general patterns of feeding established in the laboratory, and cannot be used to estimate absolute cannibalism rates or preference values: the number observed feeding varied greatly from time to time and among instars; although we made frequent observations, few *Notonecta* were seen feeding on any particular date; we do not know the abundance of *Daphnia* actually available in *Notonecta*'s foraging zone (mainly the top few centimetres of the water column); finally, handling times varied greatly among prey types and predator instars and we do not have adequate data on handling times in the field.

For an index of the potential cannibalism rate of populations of *Notonecta,* we used the cannibalism rates by instars III to adult as estimated in the laboratory. These instars are cannibalistic in the laboratory and field, instar V having the highest cannibalism rate (present results, Fox 1973, Scott 1980). Young adults and instar IV cannibalized at about the same rate (Fig. 1), but adult feeding rate declines with age and old adults cannibalize weakly (Scott 1980, Chesson 1981). Cannibalism rates from Scott's (1980) experiments averaged over treatments with preferred and nonpreferred alternative prey available, were used to assign a cannibalism index to each of the larger instars, setting adults = 1, on the assumption that the adult group consisted of equal numbers of old and young. The other indices are then: instar III: 0.5, instar IV: 1.3, instar V: 2.6.

Stock tank experiments

Notonecta *phenology.*—The original adult population declined steadily in numbers through the experiment (Fig. 2). Close to half survived to the end in most populations, and there was no significant effect of either food supply (i.e., *Drosophila*) or their own density on the number surviving (Table 4). Although the percentage of adults surviving was highest in the high food–low adult density treatment, this result was based on only 12 individuals.

Per capita reproduction was somewhat higher in every treatment during the initial period of egg production (until the 10th census, reflecting ≈15 d of egg production) than during the remainder of the experiment, but this difference was not statistically significant (Table 5).

The earliest first instars produced from eggs laid during the experiment (the new cohort) appeared after the census on day 14; the first to survive to the adult stage appeared around day 60, as indicated by the increase in the total number of old plus new adults in low-density treatments, most obviously in the high-food treatment (Fig. 3). Most of the cohort had either died or reached the adult stage by the end of the experiment. None of the new adults could have produced first instars before the end of the experiment given the time required for maturation of the adult and the development of eggs (Fox 1973, 1975*b*). Reproduction (as measured by recruitment of first instars, see Methods: Calculation of *Notonecta* Vital Rates) extended somewhat later into the season in high food treatments (Fig. 4). Populations within a treatment showed broadly similar phenology, but differed in detail.

Population convergence, overconvergence, and food supply

Within each tank one side had a high initial *Notonecta* density and the other had a low initial density. There are several different components of these populations that might converge to a putative equilibrium density, including total *Notonecta* at the end of the experiment, and potential number of adults in the new cohort surviving to overwinter. The latter is the better choice for our purposes since old adults (i.e., survivors from the initial cohort) lose vigor and stop reproducing

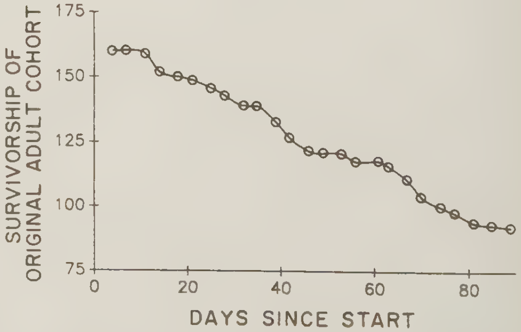

Fig. 2. The number of the original cohort of adult *Notonecta,* summed over all tanks, surviving from the start of the experiment to successive census days.

TABLE 4. Effect of prey (*Drosophila*) density and adult *Notonecta* density on the survivorship of the original cohort of adult *Notonecta* in the stock tanks.

A. Total number of adult *Notonecta* in each treatment surviving or dying out of the original adult cohort by the end of the experiment (totals over all replicates).

	High *Notonecta* density			Low *Notonecta* density		
	Alive	Dead	Percent surviving	Alive	Dead	Percent surviving
High *Drosophila*	34	30	53	12	4	75
Low *Drosophila**	25	23	52	7	5	58

B. Log-linear analysis of numbers surviving vs. dying.

Source of variation†	χ^2	df	*P*
Notonecta	1.83	1	.18
Drosophila	0.79	1	.38
Notonecta × *Drosophila*	0.63	1	.43

* Note there were only three tanks in the low *Drosophila* food level; there were four tanks in the high food level.

† A significant main effect indicates survival differed between the two levels of a factor. A significant interaction indicates there were unique effects associated with some treatment combinations of the two factors.

as they age; they probably do not survive and contribute to the production of a new generation the next year (Fox 1975*b*, Scott 1980).

To obtain the total number of overwintering adults, we added to the number of new adults produced the number of extant immatures (most of which were instar V), corrected by expected survivorship to adulthood, based upon the average through-stage survival rates over the experiment. This potential number of new adults is henceforth the "overwintering" population.

There was convergence in the overwintering populations in both food (*Drosophila*) treatments: the relative difference in the number of overwinterers between the high- and low-density treatments was less at the end than at the beginning of the experiment for both food treatments (Table 6A). (This was determined by showing that the final logarithmic differences were, on average, significantly smaller than the initial logarithmic difference, namely 1.39.)

There was also overconvergence in both food treatments. In fact, for every pair of populations housed on opposite sides of a single tank, the low-density population produced more overwinterers than the high-density population (Table 6A).

If we consider total adults (i.e., including old adults: Fig. 3, bottom panels show an example) or total "big" *Notonecta* (instars IV–VI), statistically significant convergence is still evident (Table 6B). The clear overconvergence seen in the overwintering population, however, was not seen in total adults or big *Notonecta* (Table 6B). The failure to see overconvergence in total adults arises from the following combination. New adults overconverged, but old adults showed no convergence: their survival was independent of *Notonecta* density or food level (Table 4).

TABLE 5. Fecundity (viable eggs per day per female) as estimated from recruitment of instar I. For these analyses, the experiment was broken into the two time periods. The first is the initial period of egg production, which includes approximately the first 15 d of egg production, the second is the remainder of the experiment.

A. Fecundity for each treatment ($\bar{X}$ ±1 SE)

	First time period		Second time period	
	Low *Notonecta* density	High *Notonecta* density	Low *Notonecta* density	High *Notonecta* density
Low *Drosophila*	2.35 ± 0.38	0.92 ± 0.22	1.62 ± 0.14	0.89 ± 0.24
High *Drosophila*	3.38 ± 0.22	1.85 ± 0.17	2.13 ± 0.49	1.71 ± 0.21

B. Summary of repeated-measures ANOVA on log-transformed fecundity

Source of variation	*F*	df	*P*
Time period	2.4	1,5	.18
Notonecta density	23.4	1,5	.005
Drosophila level	24.1	1,5	.004
Time period × *Notonecta* density	4.0	1,5	.10
Time period × *Drosophila* level	0.2	1,5	.71
Notonecta density × *Drosophila* level	3.1	1,5	.14
Time periods × *Notonecta* density × *Drosophila* level	0.1	1,5	.74

TABLE 6. Demonstration of convergence and overconvergence in density by experimental *Notonecta* populations set initially at high or low density, and given either a high or low food supply.

A. Estimated number of overwintering adult *Notonecta* in each tank and treatment, and tests of convergence between high and low *Notonecta* density treatments.

Food treatment	Tank no.	High *Notonecta* side (initial $N = 16$)	Low *Notonecta* side (initial $N = 4$)	Difference of logs (initially = 1.39)
High *Drosophila*	10	7.3	14.2	−0.66
	13	8.6	12.6	−0.38
	21	4.9	12.2	−0.89
	25	8.3	11.0	−0.28
	$\bar{X}$ ± SE	7.3 ± 0.83	12.5 ± 0.66	−0.56 ± 0.14
Low *Drosophila*	2	3.2	5.9	−0.61
	6	1.2	6.7	−1.71
	17	1.4	3.3	−0.85
	$\bar{X}$ ± SE	1.9 ± 0.6	5.3 ± 1.03	−1.06 ± 0.33

Tests on differences of log densities between initially high- and initially low-density sides of each tank. High- and low-*Drosophila* treatments are combined.

	H_1	t_6	P
Convergence	$\mu < 1.39$	−12.1	<.001
Overconvergence	$\mu < 0$	−4.3	<.001

B. Number ($\bar{X}$ ±1 SE) of total adult and big (instars IV–VI) *Notonecta* in each treatment at the end of the experiment.

	High *Notonecta* density		Low *Notonecta* density	
	Adult	Big	Adult	Big
High *Drosophila*	12.3 ± 2.0	17.0 ± 1.1	14.5 ± 1.2	15.8 ± 1.0
Low *Drosophila*	9.0 ± 1.7	10.7 ± 1.3	5.0 ± 0.6	8.0 ± 0.6

Tests on differences of log densities between initially high- and initially low-density sides of each tank. High- and low-*Drosophila* treatments are combined.

		Adult		Big	
	H_1	t_6	P	t_6	P
Convergence	$\mu < 1.39$	−22.0	<.001	−7.69	<.001
Overconvergence	$\mu < 0$	+2.86	>.1	+0.81	>.1

Mechanisms of convergence and overconvergence

Since these were closed populations, dynamics were determined entirely by natality and mortality. No eggs were ever observed to be eaten by *Notonecta*, and egg viability was consistently high (92%) and unaffected by the treatments (two-way ANOVA, $P > .1$ for treatment and interaction effects). Thus the recruitment of instar I to the population reflected the production of eggs.

Fecundity (viable eggs per female per day) contributed to convergence and overconvergence. It was responsive to both adult density and food supply, especially in the low-food treatments, both during the early part of the experiment and in the later part, when egg production seemed somewhat lower (Table 5). During the initial period, the low-*Notonecta* adults at high food had fecundity (3.4 ± 0.2 eggs/d) exceeding the maximum we have observed in the laboratory (in *Notonecta* fed excess food at 25°C Fox [1975*b*] reports a maximum of 2.3 ± 1.2 eggs/d but in one experiment Fox [1973] observed 3.6 eggs/d), and thus their fecundity was not food limited. The high-*Notonecta* adults at high food had fecundity about half (55%) as high as the low-*Notonecta* treatment and thus may have been somewhat food limited. At low food levels, fecundity was 24–50% lower than at the high-food level (Table 5).

Although fecundity was both density dependent and food dependent, we were not able to detect a significant food level × *Notonecta* density interaction ($P = .14$, Table 5B). The results suggest, however, that density-dependent fecundity had more pronounced effects in the low-food tanks: during the first time period, in the high-food treatments fecundity in the high-density populations was 55% of that in the low-density populations, whereas in the low-food populations this figure was 39%. The comparable numbers in the second time period were 80 and 55%. These differences played a role in convergence of the overwintering populations: over the entire experiment, in the high-food tanks, the high-*Notonecta* density produced nearly three times as many instar I recruits as the low-*Notonecta* density, while at low food the numbers produced at the two *Notonecta* densities were roughly equal (Fig. 5). Note that at both food levels the high-*Notonecta* density started with four times as many adult females, yet produced less than four times as many instar I recruits as the corresponding low-density treatment.

Subsequent mortality of first instars (low-food) and

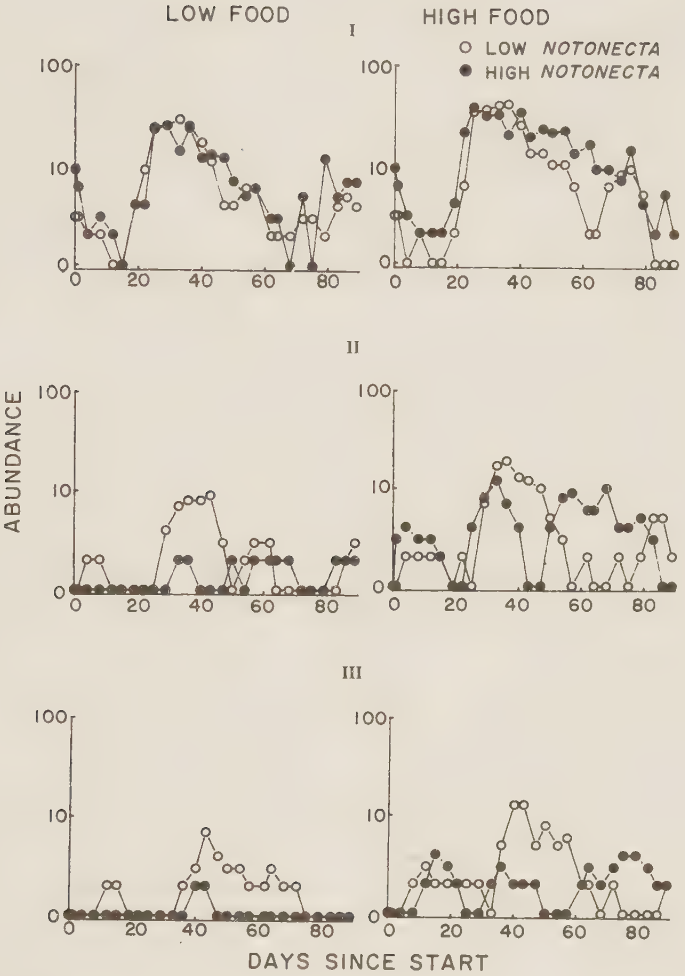

FIG. 3. Examples of the population dynamics (numbers plotted against days since the start of the stock tank experiment), by instar, seen in each treatment. Dynamics for the different initial *Notonecta* densities within a food level come from the opposite sides of the same tank. For all instars the total number present is shown; for instars I and VI this can include some individuals that were present at the start of the experiment as well as new recruits.

first and second instars (high-food) completed the process of convergence (and of overconvergence) (Fig. 5). Through-instar survival (i.e., the fraction entering the instar and surviving to molt) in the first instar was especially low, and was significantly and strongly density dependent (Table 7B). Although survival in instar II was not significantly density dependent overall, it was significantly density dependent in the high-*Drosophila* treatment ($P < .05$, pairwise contrast using common covariance structure [SAS 1985]), where survival in the high-density *Notonecta* treatment was only half of that seen in the low-density populations (Table 7A). Survival was high in the later stages with no indication of significant differences among treatments (Table 7B).

Overconvergence occurred very quickly: as a result of these strongly density-dependent processes, the cumulative numbers recruited were actually higher for the low initial *Notonecta* density treatments than for the high-density treatments by the second instar in low-food tanks, and by the third instar in high-food tanks (Fig. 5). Overconvergence was maintained thereafter (Table 6).

The agent of density-dependent mortality upon instars I and II was cannibalism by large-instar *Notonecta*. The evidence is of several sorts. First, most of

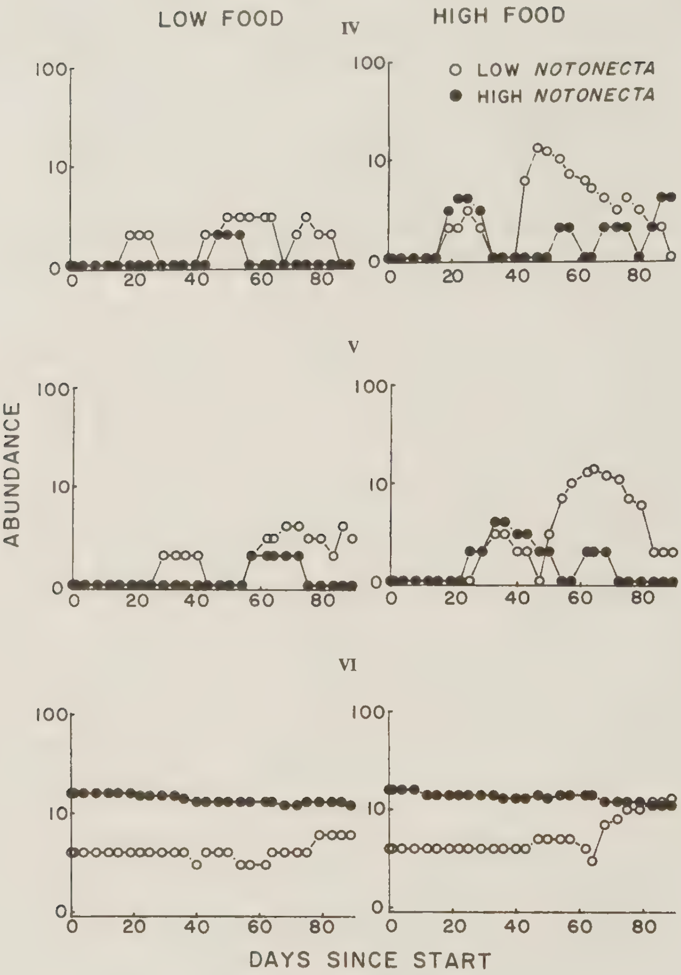

FIG. 3. Continued.

the time, instar I and II corpses had holes characteristic of those made by larger *Notonecta.*

Second, the instantaneous per capita mortality rates of instars I and II were positively related to the abundance of cannibalistic *Notonecta* (Table 8). We tested for this by regressing a mortality index (the proportion of individuals in instar I or II observed during a week that did not survive to the end of that week) against the weighted number of cannibals present (using the cannibalism indices calculated above from laboratory experiments). The results show that mortality of instar I increased significantly with increased density of cannibals in both food treatments, and this was also true for instar II in the high-food treatment, but not the low-food treatment (Table 8). This last result is consistent with our observations on population dynamics and through-instar mortality described above. (Through-instar mortality of instar II was higher in the high-adult-*Notonecta* density treatment than in the low-adult density treatment only in high-food tanks, and convergence was essentially complete by instar II at low food, but continued through to instar III at high food.)

Third, as expected, mortality of instar I increased with increasing density of cannibals significantly faster at low food than at the high food (see comparison of slopes, Table 8); thus the impact of a cannibal was lessened in the presence of alternative food.

It is possible that the small instars were actually eaten after they died from other causes, the most likely alternative cause of death being inadequate food. It appears, however, that food for the early instars was always in excess. First, we showed above that the most important alternative prey for young *Notonecta* was

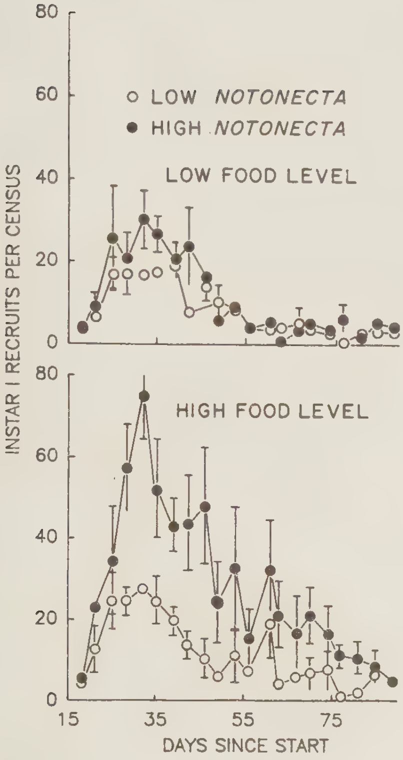

FIG. 4. The estimated instar I recruitment per census (means ± 1 SE) plotted against days since the start of the stock tank experiment.

Daphnia (Tables 1 and 3), and that *Daphnia* density did not vary among treatments (Methods: Experimental Design). Second, based on the time between either peak abundances of successive instars or the appearances of the first few individuals of successive instars, we estimate that instars I and II lasted ≤7 d. Thus they developed as fast as the maximum rate observed in the laboratory at 25° (between 6 and 7 d) and in the presence of greatly excessive food (Fox 1973). Although this rapid development combined with our sampling schedule (twice a week) precludes a formal analysis, there is no evidence that the duration of these instars varied in a systematic way among treatments.

Although the above results are internally consistent, they are puzzling in one regard. A priori we expected that cannibalism on instar II would be more intense at low- than at high-food levels, as it is for instar I. But our result in Tables 7 and 8 can be interpreted as indicating that cannibalism on instar II acted more strongly at the high-food level. We feel that this interpretation is incorrect, and that our failure to see significant effects for the second instar at low food is most likely an artifact due to low statistical power. At the low-food levels fecundity was lower, as was survival through the first instar. As a consequence, very few instar II were recruited in the low-food and high-*Notonecta* populations (Fig. 5); our through-stage survival (and mortality rate) estimates are therefore quite variable in this treatment (see the relevant standard error in Table 7). In addition, for the regressions against the cannibalism index presented above, high values of the cannibalism index were absent from this treatment precisely because the action of previous density-dependent mechanisms led to fewer large *Notonecta* being produced. This restricted range of data probably contributed to the large standard error in the slope parameter for this instar (Table 8).

Based on the temporal changes in mean cannibalism index through time, and on the above regressions, it seems evident that initial differences among treatments in cannibalistic mortality are lost by about day 40 of the experiment (itself an expression of convergence; Fig. 6). The initial differences nevertheless had marked effects on the through-stage survival probabilities for instar I and, at high food, for instar II pooled over the entire experiment. The reason for this is that most recruitment into instars I and II occurred early in the experiment (Fig. 5), when initial differences in potential cannibalism were still high (Fig. 6).

DISCUSSION

There have been surprisingly few convergence experiments done since Eisenberg's (1966) study of pond snails; he showed that the equilibrium was set by the food supply and convergence occurred via food- and density-dependent fecundity. Stimson and Black (1975) and Black (1977) studied convergence in intertidal grazing limpets, whose densities were again resource limited. Lawton et al. (1986) have extended convergence studies to herbivorous insects. That study is so far unique among convergence experiments in that, apparently, predators kept the population below any resource limitation; however, no evidence is available on the mechanisms from this preliminary experiment. The *Notonecta* in the present study were again food limited. Our results provide more detail on the mechanisms of convergence than has been available before.

Populations of *Notonecta* in streams in southern Cal-

TABLE 8. Regressions of mortality rate against cannibalism index. Analyses for both instar I and II were done separately for each food level.

Instar	Food level	Slope ($\bar{X}$ ± SE)*	F	df	P
I	low	0.05 (0.01)	21.7	58	<.0001
	high	0.02 (0.005)	13.6	78	.0004
II	low	0.005 (0.02)	0.04	47	.84
	high	0.015 (0.007)	4.2	64	.04

* F tests for equality of slopes for different food levels: Instar I, F = 5.71, df = 1,136, P = .02; Instar II, F = 0.17, df = 1,111, P = .68.

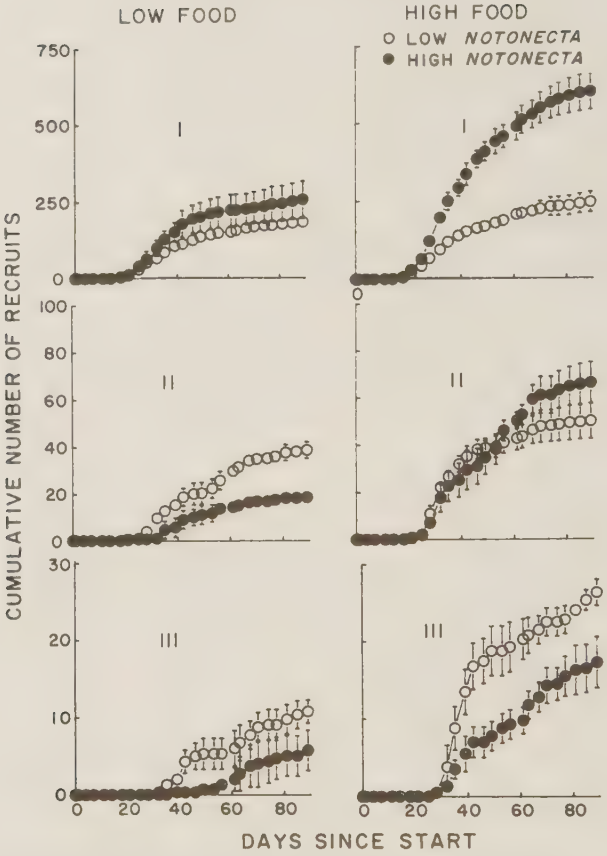

FIG. 5. Cumulative number of recruits (mean ± 1 SE) of instars I–III, plotted against days since the start of the stock tank experiment.

ifornia appeared to be strongly food limited but, as in our stock tanks, cannibalism of smaller by larger instars was the immediate mechanism of population regulation (Fox 1975*b, c*). Our experiment shows that an important feature of this mechanism is that the densities achieved by the small instars is set, not by their own food supply, but by that of the large instars. Thus, there was always excess food (zooplankton) for the first few instars; they were kept well below any limits set by this food supply because food for large instars (*Drosophila*) was sometimes limited. This situation may be common in other age- or size-structured populations. For example, later instar damselflies may often be food limited, while earlier instars feed on smaller prey that are generally abundant (Crowley et al. 1987).

Convergence to the food equilibrium was through both density-dependent fecundity, and density-dependent early mortality (cannibalism), with the action of cannibalism extending to a later stage (the second instar) at high food. Cannibalism operates so early in the victims' development that it is similar to reduced fecundity in its effects on convergence.

Cannibalism allows larger *Notonecta* to exploit indirectly a food source, the prey of smaller instars, that is otherwise largely unavailable. This could well influence the ultimate abundance of overwintering *Notonecta,* since small *Notonecta* make up a significant fraction of the diet of large *Notonecta*. However, we are unable to measure this effect.

Our results suggest that the dynamics of at least this particular polyphagous and age-structured freshwater predator can be portrayed much more simply than would appear at first sight. The primary reason for this simplicity is that the rate of supply of adult food is dynamically uncoupled from *Notonecta*'s dynamics. In natural systems, as in our experiment, this food supply is also independent of *Notonecta* dynamics: it is mainly arthropods falling onto the water surface. This adult food supply primarily determines the overwintering population of adults each year; it also primarily de-

TABLE 7. The effects of initial *Notonecta* density, and food supply, on instar-specific *Notonecta* survival rates.

A. Through-instar survival of *Notonecta* ($\bar{X} \pm 1$ SE) for each treatment.

		High *Notonecta* density		Low *Notonecta* density	
	Instar	Survival	*N*	Survival	*N*
High *Drosophila*	I*	0.12 ± 0.01	4	0.22 ± 0.03	3
	II*	0.25 ± 0.03	4	0.51 ± 0.06	3
	III	0.69 ± 0.14	4	0.71 ± 0.05	3
	IV	0.62 ± 0.10	4	0.92 ± 0.04	3
	V	0.76 ± 0.11	4	0.65 ± 0.05	3
Low *Drosophila*	I*	0.08 ± 0.02	3	0.21 ± 0.01	3
	II	0.32 ± 0.23	3	0.26 ± 0.05	3
	III	0.48 ± 0.29	3	0.57 ± 0.02	3
	IV	0.63 ± 0.37	2	0.92 ± 0.08	3
	V	1.0 ± –	1	0.56 ± 0.29	3

B. Repeated-measure ANOVA of through-instar survival. Tank is treated as a random factor nested within *Drosophila* treatment and the mean square associated with it is used as the error term for tests of the main effect of *Drosophila*. All tests used arcsine square root transformations.

Source of variation	df	SS	*F*	*P*
		Instar I		
Notonecta density	1	0.10	70.2	.0004
Drosophila	1	0.0043	0.96	.37
Drosophila × *Notonecta*	1	0.0021	1.56	.27
Tank	5	0.022	3.2	.11
Error	5	0.0069	···	···
		Instar II		
Notonecta density	1	0.054	0.85	.39
Drosophila	1	0.043	1.26	.31
Drosophila × *Notonecta*	1	0.076	1.19	.32
Tank	5	0.17	0.54	.75
Error	5	0.32	···	···
		Instar III		
Notonecta density	1	0.001	0.01	.93
Drosophila	1	0.16	0.97	.37
Drosophila × *Notonecta*	1	0.017	0.09	.77
Tank	5	0.84	0.90	.54
Error	5	0.92	···	···
		Instar IV		
Notonecta density	1	0.31	1.96	.23
Drosophila	1	0.059	0.87	.39
Drosophila × *Notonecta*	1	0.0035	0.10	.76
Tank	5	0.33	0.43	.81
Error	4	0.63	···	···
		Instar V		
Notonecta density	1	0.26	2.66	.20
Drosophila	1	0.02	0.08	.80
Drosophila × *Notonecta*	1	0.07	0.77	.44
Tank	5	1.34	2.78	.21
Error	3	0.29	···	···

* Indicates cases where survival differed between high and low *Notonecta* density within a food treatment ($P < .05$); these pairwise tests differ from an ordinary one-sample *t* test only in that the common variance from the ANOVA (see Table 7B) was used in the tests. These pairwise tests were done separately for each instar at each *Drosophila* level.

termines the peak population (which consists largely of small instars) and the general level of *Notonecta* density between peak abundance and the end of the season.

Notonecta's dynamics resemble, at least in one respect, those of open populations (i.e., those, such as barnacles, whose recruits come from elsewhere) in that the equilibrium is determined, in part, by an external "forcing function." In *Notonecta*, the supply of food comes from outside the local system, and the recruitment of new individuals depends, in large part, upon this food supply, as does the final equilibrium density. In open populations, the recruitment of new individuals comes from outside the local population, and this uncoupled input can affect the equilibrium (e.g., Roughgarden et al. 1985, Bence and Nisbet 1989). Examples come from reef corals (Hughes 1984), reef fish (Warner and Hughes 1989), intertidal barnacles (Gaines and Roughgarden 1985), and some aquatic insects, like mosquitoes, with a flying adult stage (Frogner 1980).

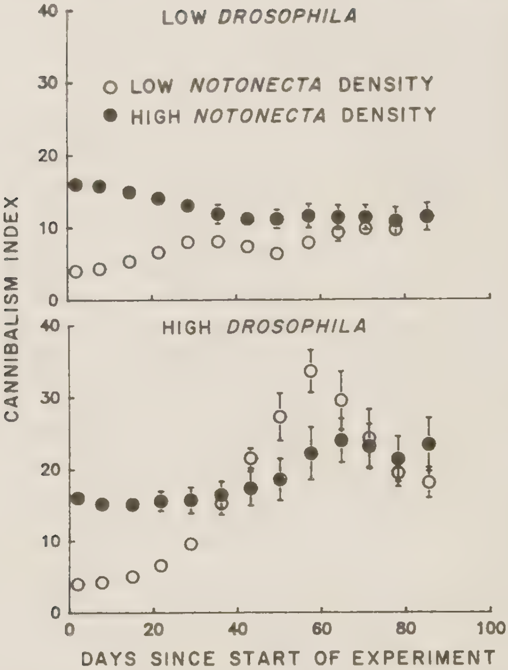

FIG. 6. Mean (±1 SE) cannibalism index (see Results: Mechanisms of Convergence and Overconvergence) plotted against days since the start of the stock tank experiment.

It is not clear how unusual these features of *Notonecta* dynamics are in other closed populations. For example, the rate of adult food supply to some other freshwater predators, such as water striders, or surface-feeding fish species can be largely independent of the dynamics of the predators (e.g., Moyle 1976, Murdoch and Bence 1987), but there are other predatory species that feed entirely upon resident prey species.

A secondary, but interesting, component of the regulation of density involves time lags in the *Notonecta* population itself. Although the density of the large-instar population is regulated by food supply, this regulation occurs during the production of eggs or the survival from cannibalism of the resulting small instars. Thus, regulation occurs through the food supply that was available to an earlier cohort of larger individuals. Particularly important, however is that only the fecundity of that cohort is sensitive to food supply; its survival seems relatively unresponsive to variation in food (perhaps, in part, because it can cannibalize its own products [Polis 1981]). It is this insensitivity that causes overconvergence: when the old adults are above the equilibrium, they survive and suppress the subsequent cohort, causing it to undershoot the equilibrium. As a result, an abundant adult cohort produces a small succeeding overwintering cohort, while a low-density adult cohort produces a relatively large overwintering cohort. Thus, if food supply were to remain relatively constant, alternating high and low populations could result. There are now several examples in nature of cyclic fluctuations in population density that appear to result from one cohort suppressing future recruits (Gaines and Roughgarden 1985, McCauley and Murdoch 1987, Nisbet and Bence 1989). The nature of such cycles appears to depend upon a variety of factors, and we intend to explore the possibility for cyclic fluctuations in *Notonecta*'s population density through modelling of its dynamics.

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LITERATURE CITED

Bence, J. R., and W. W. Murdoch. 1986. Prey-size selection by the mosquitofish: relation to optimal diet theory. Ecology **67**:324–336.

Bence, J. R., and R. M. Nisbet. 1989. Space limited recruitment in open systems: the importance of time delays. Ecology **70**:1434–1441.

Black, R. 1977. Population regulation in the intertidal limpet *Patelloida alticostata* (Angas, 1865). Oecologia (Berlin) **30**:9–22.

Chesson, J. 1981. The role of alternative prey in the control of mosquitoes by notonectids. Dissertation. University of California at Santa Barbara, California, USA.

———. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology **64**:1297–1304.

———. 1989. The effect of alternative prey on the functional response of a biological control agent. Ecology **70**:1227–1235.

Crowley, P. H., R. M. Nisbet, W. S. C. Gurney, and J. H. Lawton. 1987. Population regulation in animals with complex life-histories: formulation and analysis of a damselfly model. Advances in Ecological Research **17**:1–51.

Eisenberg, R. M. 1970. The role of food in the regulation of the pond snail, *Lymnaea elodes*. Ecology **51**:680–684.

Fox, L. R. 1970. Effects of past history and experimental conditions on the functional response curve of the predator *Notonecta hoffmanni* (Hemiptera: Notonectidae). Thesis. University of California at Santa Barbara, California, USA.

———. 1973. Food limitation, cannibalism and interactions among predators: effects on populations and communities of aquatic insects. Dissertation. University of California at Santa Barbara, California, USA.

———. 1975*a*. Cannibalism in natural populations. Annual Review of Ecology and Systematics **6**:87–106.

———. 1975*b*. Some demographic consequences of food shortage for the predator, *Notonecta hoffmanni*. Ecology **56**:868–880.

———. 1975*c*. Factors influencing cannibalism, a mechanism of population limitation in the predator *Notonecta hoffmanni*. Ecology **56**:933–941.

Fox, L. R., and W. W. Murdoch. 1978. Effects of feeding history on short-term and long-term functional responses in *Notonecta hoffmanni*. Journal of Animal Ecology **47**:945–959.

Frogner, K. J. 1980. Variable developmental period: intraspecific competition models with conditional age-specific maturity and mortality schedules. Ecology **61**:1099–1106.

Gaines, S., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences, USA **82**:3707–3711.

Hastings, A. 1984. Age-dependent predation is not a simple process. II. Wolves, ungulates, and a discrete time model for predation on juveniles with a stabilizing tail. Theoretical Population Biology **26**:271–282.

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a coral reef example. American Naturalist **123**:778–795.

Lawton, J. H., M. MacGarvin, and P. A. Heads. 1986. The ecology of bracken-feeding insects: background for a biological control programme. Pages 285–292 *in* R. T. Smith and J. A. Taylor, editors. Bracken: ecology, land use and control technology. Parthenon, Carn Corth, England.

McCauley, E. F., and W. W. Murdoch. 1987. Cyclic and stable populations: plankton as paradigm. American Naturalist **129**:97–121.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley, California, USA.

Murdoch, W. W., and J. R. Bence. 1987. General predators and unstable prey populations. Pages 17–29 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Murdoch, W. W., R. M. Nisbet, W. S. C. Gurney, and J. D. Reeve. 1987. An invulnerable age class and stability in delay-differential parasitoid-host models. American Naturalist **129**:263–282.

Murdoch, W. W., and M. A. Scott. 1984. Stability and extinction of laboratory populations of zooplankton preyed on by the backswimmer *Notonecta*. Ecology **65**:1231–1248.

Murdoch, W. W., M. A. Scott, and P. Ebsworth. 1984. Effects of the general predator *Notonecta* upon a freshwater community. Journal of Animal Ecology **53**:791–808.

Nisbet, R. M., and J. R. Bence. 1989. Alternative dynamic regimes for canopy forming kelp: a variant on density-vague population regulation. American Naturalist **134,** *in press.*

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics **12**:225–251.

Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology **66**:54–67.

SAS. 1985. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Scott, M. A. 1980. The effect of the general predator *Notonecta* (Hemiptera: Notonectidae) on community structure: selective predation and the effect of alternative prey on predator systems. Dissertation. University of California at Santa Barbara, California, USA.

Scott, M. A., and W. W. Murdoch. 1983. Selective predation by the backswimmer, *Notonecta.* Limnology and Oceanography **28**:352–366.

Stimson, J., and R. Black. 1975. Field experiments on population regulation in intertidal limpets of the genus *Acmaea.* Oecologia (Berlin) **18**:111–120.

Warner, R. R., and T. P. Hughes. 1989. Population dynamics of reef fishes. Proceedings of the Sixth International Coral Reef Symposium 1. University of Queensland Press, Townsville, Australia.

Werner, E. E., and J. G. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393–426.

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U.S. Trade in Tuna for Canning, 1987

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ABSTRACT—U.S. tuna fleet activity, canned tuna processing, ex-vessel, wholesale and retail prices and imports in 1987 are described and compared to their counterparts in previous years. Industry statistics gathered from government agencies and industry contacts are presented in 14 figures and 8 tables.

In 1987, U.S. tuna fisheries delivered 253,936 short tons (tons) of tuna to U.S. canneries. Domestic deliveries of albacore (white-meat) tuna were 2,836 tons, down 20 percent from 1986 levels. Domestic deliveries of tropical (light-meat) tuna (bigeye, blackfin, bluefin, skipjack, and yellowfin) were 251,000 tons, up 12 percent. Contract prices for tuna delivered by U.S. vessels to U.S. canneries increased dramatically in 1987. Depending on the size of fish in the delivery, ex-vessel prices of white-meat tuna increased as much as 27 percent, and prices of light-meat tuna increased as much as 47 percent.

U.S. cannery receipts of imported and domestically caught raw frozen tuna for canning totaled 532,704 tons in 1987, up 2 percent from 1986 levels. U.S. cannery receipts of white-meat tuna were 104,197 tons, down 10 percent from 1986. Imports made up 97 percent of the total cannery supply. Total 1987 U.S. cannery receipts of raw, frozen light-meat tuna were 428,507 tons, up 5 percent from 1986 levels. Imports made up 41 percent of the total cannery supply.

The 1987 U.S. pack of canned tuna was 33.6 million standard cases, up 3 percent from 1986. The pack of white-meat tuna was 7.2 million standard cases, down 11 percent from 1986; the pack of light-meat tuna was 26.4 million standard cases, up 7 percent. U.S. imports of canned tuna in 1987 were 10.8 million standard cases, down 11 percent from 1986 levels, the first time in recent years that imports have declined. Per capita consumption of canned tuna in the United States was 3.5 pounds in 1987, down slightly from 1986. The retail composite price was $2.26 per pound, unchanged from 1986.

Introduction

The U.S. canned tuna harvesting/processing industry is an active participant in the global tuna industry. In 1986 U.S. vessels took 8 percent of the total world catch of all tuna species[1]. Having developed canned tuna processing in the early 1900's, the U.S. processing sector is the world leader accounting for 36 percent of total world canned tuna production in 1986. The United States continues as the major world market for canned tuna, consuming 34 percent of total world production in 1987.

The United States, along with Japan, Spain, and France, other historically dominant tuna harvesting and processing nations, have in recent years met increasing competition from rapidly expanding tuna industries in southeast Asia, Latin America, the western Pacific, and Africa. The world tuna catch was 3,768,000 short tons (tons) in 1986, an increase of 39 percent from 1979. However, while catches in the historical tuna countries increased 24 percent, catches in developing countries increased 53 percent. U.S. landings increased 14 percent over the period. In 1986, the United States was fourth in volume of tuna catches behind Japan, Indonesia, and the Philippines.

Global production of canned tuna was 775,000 tons in 1985, 16 percent above 1979 production. As for catches, this growth is concentrated in developing nations where, from 1979 to 1985, canned tuna production increased 86 percent. In contrast, production increased 5 percent in the historical tuna nations. Canned tuna production in the United States decreased slightly between 1979 and 1985 then increased in 1986. The United States continues as the leading processor of canned tuna.

International trade in raw tuna and canned tuna products has also increased, paralleling the increases in fishing and canning sectors. In 1986, 861,000 tons of fresh and frozen raw tuna were traded by major trading nations, an increase of 47 percent over 1979 levels[2]. The major growth has been in developing countries where raw tuna imports increased 316 percent between 1979 and 1986. Raw tuna imports to developed countries increased only 4 percent and U.S. imports actually declined 2 percent over the period. The United States accounted for 24 percent of total world imports of raw tuna for canning in 1986.

World canned tuna producers exported 315,000 tons of canned product in 1985, up 140 percent from 1979. Virtually all this growth has been in developing countries. The United States continues as the major world importer of canned tuna. U.S. imports were 92,500 tons in 1986, up 215 percent from 1979.

This is the sixth annual review of the U.S. tuna canning industry (Herrick, 1984; Herrick and Koplin, 1984; Herrick and Koplin, 1986; Herrick and Koplin, 1987; Herrick, et al.[3]). In the following sections we describe the industry's performance in 1987. In the first section we

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[1] Food and Agriculture Organization of the United Nations. GLOBEFISH, a computerized system of market information.

[2] In 1987, 97 percent of the raw tuna traded was traded by, in order of volume, the United States, Thailand, Japan, Italy, the Ivory Coast, Singapore, Senegal, France, Spain, Ghana, and Portugal.

Table 1.—U.S. cannery receipts (short tons) of raw tuna by processing site and direct exports, 1982-87[1].

	California/American Samoa/Hawaii						C/AS/H	Puerto Rico						P.R.
	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
Domestic														
Albacore	6,965	10,466	10,323	5,608	3,231	1,971	7,318		4	3,565	1,245	296	865	1,022
Skipjack	82,669	113,465	94,152	66,716	71,803	75,210	85,762	18,781	41,608	51,441	17,304	18,802	12,105	29,587
Yellowfin[2]	93,468	90,052	59,907	35,365	57,120	83,524	67,182	24,800	30,044	35,193	87,571	75,941	80,261	50,710
Subtotal	183,102	213,983	164,382	107,689	132,154	160,705	160,262	43,581	71,656	90,199	106,120	95,036	93,231	81,319
Imported														
Albacore	33,928	22,750	21,962	20,030	25,811	25,468	24,896	60,670	50,105	70,882	75,122	86,481	75,893	68,652
Skipjack	45,837	50,633	28,737	18,026	18,590	22,618	32,365	82,178	84,675	106,136	74,606	86,441	72,440	86,807
Yellowfin[2]	17,811	14,081	12,685	10,169	11,875	18,384	13,325	33,402	24,251	29,045	57,192	67,260	63,965	42,230
Subtotal	87,576	87,464	63,384	48,225	56,276	66,427	70,586	176,250	159,031	206,063	206,920	240,182	212,298	197,689
Grand total	280,678	301,447	227,766	155,914	188,430	227,175	230,848	219,831	230,687	296,262	313,040	335,221	305,529	279,008

	Direct exports[3]						Dir.exp.	Total						Overall
	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
Domestic														
Albacore	62		108			841	34	7,027	10,470	13,996	6,853	3,527	3,677	8,374
Skipjack	387	45	15,388	19,669	22,207	16,256	11,539	101,837	155,118	160,981	103,989	112,812	103,571	126,888
Yellowfin[2]	3,864	538	16,980	15,128	11,539	12,866	9,610	122,132	120,634	112,080	138,064	144,600	176,651	127,502
Subtotal	4,313	583	32,476	34,797	33,746	29,963	21,183	230,996	286,222	287,057	248,606	260,939	283,899	262,764
Imported														
Albacore								94,598	72,855	92,844	95,152	112,292	101,361	93,549
Skipjack								128,015	135,308	134,873	92,632	105,031	95,068	119,172
Yellowfin[2]								51,213	38,332	41,730	67,361	79,135	82,349	55,554
Subtotal								273,826	246,495	269,447	255,145	296,458	278,768	268,275
Grand total	4,313	583	32,476	34,797	33,746	29,963	21,193	504,822	532,717	556,504	503,751	557,397	562,667	531,039

[1] Includes imported and domestically caught tuna destined for canning, excludes U.S.-caught tuna destined for export or for the fresh market; excludes imported tuna destined for the fresh tuna market or designated as flakes and not fit for human consumption.
[2] Includes bigeye, blackfin, and bluefin tuna.
[3] Includes tuna landed directly or transshipped to a foreign country; excludes tuna exported from the U.S. east and west coasts.

review the U.S. albacore fishery and U.S. processing of white meat tuna in 1987. In the second section we focus on the fishery for tropical tunas and processing of light meat tuna. In the third section we describe U.S. imports of canned tuna and, in the fourth, consumption of canned tuna.

White Meat (Albacore) Tuna

Albacore, *Thunnus alalunga*, is the only species that may be canned as white meat tuna in the United States[4]. About 21 percent of the total U.S. tuna pack in 1987 was white meat tuna.

Production by the U.S. Albacore Fleet

The U.S. albacore fleet consists of about 1,800 vessels, of which about 250 land 90 percent of the catch in any given year (Majors[5]). About 80 percent of the vessels use jig gear, 10 percent pole-and-line gear, and 10 percent either a combination of jig and pole and line or other gear (e.g., gill net). The fleet operates exclusively in the Pacific Ocean. Before 1974, reported catches were taken exclusively within 300 miles of the North Pacific coast of North American from central Baja California to British Columbia (Majors, 1987). As a result of joint NMFS/American Fishermen's Research Foundation (AFRF) exploratory fishing in 1975, larger jigboats in the fleet expanded their operations to areas northwest of Hawaii in the late 1970's and early 1980's. In 1986 and 1987, NMFS/AFRF exploratory fishing located new fishing grounds in the South Pacific. Since then, larger U.S. jigboats have fished in this new area east of New Zealand.

Receipts at U.S. canneries in 1987 of albacore caught by U.S. fishermen continued a decline from a recent high in 1984 (Fig. 1)[6]. Receipts (2,800 tons) were 20 percent less than 1986 receipts and 66 percent less than recent average (1982-86) receipts (Table 1).

Sixty-nine percent of the receipts of

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[3] Herrick, S. F., W. W. Parks, and P. J. Donley. 1988. U.S. tuna trade summary, 1986. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Reg. Admin. Rep. SWR-88-3, 23 p.

[4] U.S. Government Printing Office, 1985. 21 Code of Federal regulations. Section 161.190(a) (4) (i).

[5] Majors, Tony. 1989. Fishery biologist, NMFS Southwest Fisheries Center, La Jolla, CA 92038. Personal commun., March.

[6] Principal U.S. receiving and processing sites for both white and light meat tuna in 1987 were Mayaguez and Ponce, Puerto Rico; San Pedro, California; and Pago Pago, American Samoa. For reporting purposes, receipts and production data are combined for American Samoa and California.

Table 2.—U.S. cannery ex-vessel (contract) prices (U.S. dollars/short ton) at California/American Samoa/Puerto Rico, 1980-87[1].

Year and period[2]	Albacore		Skipjack				Yellowfin				
	>9 lb.	<9 lb.	>7.5 lb.	4-7.5 lb.	3-4 lb.	<3 lb.	>20 lb.	7.5-20 lb.	4-7.5 lb.	3-4 lb.	<3 lb.
1980											
B	1,610	1,610	850	850	700	545	950	950	810	810	810
E	1,635	1,635	1,100	1,100	1,000	800	1,200	1,200	1,100	1,100	1,100
1981	1,800	1,800	1,100	1,100	1,100	800	1,200	1,200	1,100	1,100	1,100
1982											
B	1,425	1,425	1,100	1,100	1,100	800	1,200	1,200	1,100	1,100	1,100
M			1,040	1,040	940	740	1,140	1,140	1,040	1,040	1,040
E	1,225	1,000	890	890	700	500	1,170	1,050	890	890	890
1983											
B			950	850	700	420	1,230	1,050	850	700	420
M	1,250	975	900	800	640	420	1,125	990	800	640	400
E			880	780	585	250	1,125	975	780	585	250
1984											
B	1,400	1,125	830	730	500	250	1,085	950	730	500	250
M			850	750	550	250	1,000	900	750	550	250
E	1,150-1,300	875-1,025	763	650	470	235	925	800	650	470	235
1985											
B			708	610	435	200	865	753	610	435	200
M	1,300	950	738	640	500	275	870	758	640	500	275
M	1,150	800	650	590	490	290	815	715	590	490	290
E	1,000	800	700	630	500	300	825	725	630	500	300
1986											
B	1,100	750	700	630	500	300	780-800	700	630	500	300
M			685	615	485	285	765	685	615	485	285
E			700	630	500	300	780	700	630	500	300
1987											
B	1,235	950	685-700	615-630	485-500	283-300	765-780	685-700	615-630	485-500	285-300
M	1,400	950	700-750	630-700	500	300	780-880	700-750	630-700	500	300
M			750	700	500	300	880	750	700	500	300
E			1,000	937	725	450	1,125	1,000	937	725	450

[1] Contract prices may be adjusted at the time of unloading depending upon salt content, temperature of the fish, physical consition of the fish, and other quality criteria.
[2] Period: B = beginning of year, M = midyear (various dates), E = end of year.

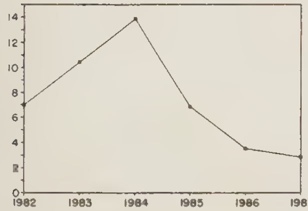

Figure 1.—Deliveries of albacore to U.S. canneries by U.S. fishermen, 1982-87.

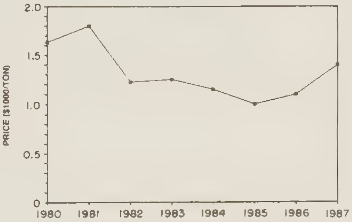

Figure 2.—Contract price for representative size (9 lb and over) albacore paid by U.S. canneries to U.S. fishermen at the end of the year, 1980-87.

Table 3.—U.S. cannery ex-vessel (weighted) prices (US$ per short ton), for domestically caught tuna, 1980-87.

Year	Albacore		Skipjack		Yellowfin	
	Nominal	Real[1]	Nominal	Real[1]	Nominal	Real[1]
1980	1,659	1,929	1,063	1,236	1,180	1,372
1981	1,800	1,908	1,030	1,092	1,170	1,241
1982	1,387	1,387	965	965	1,123	1,123
1983	1,268	1,220	799	769	1,032	993
1984	1,252	1,160	760	704	982	910
1985	1,087	975	622	558	820	735
1986	1,108	968	616	538	743	649
1987	1,496	1,273	716	609	892	759

[1] Adjusted for inflation using GNP implicit price deflator (1982 = 100).

domestically caught albacore delivered to U.S. canneries was received at canneries in American Samoa and California (Table 1). The remaining 31 percent was transshipped to Puerto Rico from west coast ports. In addition, 841 tons of albacore caught by U.S. fishermen in the new south Pacific troll fishery were exported through Tahiti, and an additional 300-400 tons were landed at west coast ports and then exported to Fiji and Japan.

The contract price for domestically caught albacore received at U.S. canneries increased dramatically in 1987 (Fig. 2). The contract price was $1,235 per ton for large fish (9 pounds and larger) at the beginning of 1987, 12 percent greater than the price at the beginning of 1986 (Table 2). The price for small fish (<9 pounds) was $950 per ton, 27 percent greater than the 1986 price. By mid-year, the contract price had risen to $1,400 per ton for large fish. According to industry sources, the general shortage of fish led to canners offering incentives and bonuses for albacore which brought the actual price well over $1,500 per ton.

Price increases offset the decline in landings, and aggregate ex-vessel revenue from the 1987 albacore fishery was 41 percent above that of 1986. Average ex-vessel price (total ex-vessel revenue divided by total domestic cannery receipts) was $1,496 per ton for U.S.-caught albacore in 1987, a 35 percent gain from 1986 (Table 3). The real (inflation

Table 4.—U.S. cannery imports of raw tuna (short tons) by country of origin, 1982-87.

	1982		1983		1984		1985		1986		1987	
Source[1]	White	Light[2]	White	Light	White	Light	White	Light	White	Light	White	Light
Brazil	1,443	16,181	1,186	15,154	2,018	7,743	710	15,282	218	12,327	373	3,823
Canary Islands	1,693	1	7,653	5	14,030	10	9,415	16	9,184	20	5,802	9
Cayman Islands		6,723				9,960		11,031		8,606		4,706
Ecuador				2,809		12,034		18,722		16,365		12,018
Ghana	1,078	27,783	345	23,751	170	6,640						
Ivory Coast		27,862		13,783	289	30,997		15,887		23,549	297	23,090
Japan	5,834	12,705	696	18,426	10,946	20,965	6,754	718	4,396	922	1,188	
Mauritius	4,811		4,668		5,026		5,769		6,706	12	8,059	87
Mexico										3,331		19,406
Netherlands Antilles	10,054	1,998	8,560	258	9,619	298	12,110	197	14,723	442	8,246	255
Panama		29,558	1	8,110	424	13,928		15,136		24,684		7,206
Philippines		5,923		6,476		1,327						
Reunion	12,036	146	7,438	3	4,363	67	1,521	756	3,605	232	2,629	2,643
Seychelles				3,042		8,257	262	17,064		30,866	51	27,506
Singapore	1,386	3,846	4,217	3,761	5,024		2,562		284		6,022	
Solomon Islands		928		10,600		15,836		3,390				9,068
South Africa	17,044	1	7,304	239	11,856	1,478	21,101		26,905	1	23,194	2
South Korea	1,001	6,891	5,374	13,830	2,119	11,064	8,874	9,747	11,406	20,673	10,920	23,942
Taiwan	99	384	5,075	3,851	9,739	9,468	5,947	10,592	11,283	3,324	13,689	4,073
Uruguay	8,835	670	4,480	143	3,228	722	7,425	1,997	9,652	26	6,237	2
Venezuela		2,421	1	6,604		7,002	147	33,538	28	27,450	6	18,675
Other	29,285	35,209	15,858	42,795	13,993	16,807	12,535	5,918	13,898	11,337	14,648	20,786
Total	94,599	179,228	72,855	173,640	92,844	176,603	95,152	159,993	112,292	184,166	101,361	177,407

[1] The flag of the catcher vessel, country of export, or country though which the tuna is transshipped.

[2] Includes bigeye, blackfin, bluefin, skipjack, and yellowfin tunas.

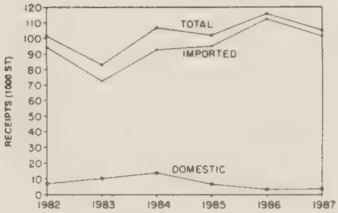

Figure 3.—Receipts of albacore by U.S. canneries by source, 1982-87.

adjusted) ex-vessel price increased 32 percent in 1987, the first increase in the period 1980-87.

U.S. Processing of Canned White Meat Tuna

Total receipts (U.S.-caught plus imports) of albacore at U.S. canneries in 1987 were 104,197 tons, 10 percent less than 1986 receipts but 3 percent above recent (1982-86) average receipts (Fig. 3, Table 1). Of the total receipts, 74 percent were delivered to canneries in Puerto Rico, and 26 percent went to canneries in American Samoa and California. Receipts at all locations were down in 1987.

As in each of the last 6 years, imports made up the bulk (97 percent) of U.S. cannery receipts of raw albacore in 1987 (Fig. 3). Imports totaled 101,361 tons, a 10 percent decrease from 1986 (Table 1). Puerto Rico was the major receiving site for albacore imports with 75 percent of the total; American Samoa and California received the remainder. Imports received in Puerto Rico were 12 percent less than in 1986; imports received in American Samoa and California were essentially the same as in 1986.

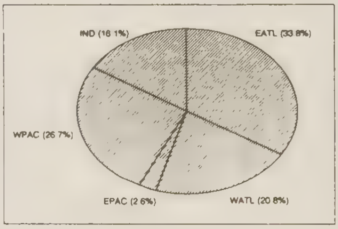

Figure 4.—U.S. cannery receipts and direct exports of albacore by ocean of origin, 1982-87 (EATL = Eastern Atlantic Ocean; WATL = Western Atlantic Ocean; EPAC = Eastern Pacific Ocean; WPAC = Western Pacific Ocean; IND = Indian Ocean).

Foreign-caught tuna entering the United States is listed by U.S. Customs as an export of the shipping nation. In the case of transshipments, the shipping country may not be the harvesting country. This is the case in 1987, for which the principal transshipping nation for albacore imports was South Africa which does not export fish taken by its own vessels to the United States (Table 4). South Africa has been a principal point for albacore transshipped to the United States since 1982 and accounted for 23 percent of total imports in 1987. Although the United States has embargoed imports of most South African products, transshipments of tuna caught by Taiwanese and Japanese albacore vessels have been permitted. Other important transshipping nations included Taiwan and South Korea.

The value of imported raw albacore at U.S. canneries in 1987 was $159.9 million, down 2 percent from 1986[7]. This corresponds to a weighted average price of $1,578 per ton, 9 percent above the average price in 1986.

As in 1985 and 1986, the Atlantic Ocean was the source of most albacore received by U.S. canneries in 1987, followed by the Pacific and Indian Oceans (Fig. 4).

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[7] Values of raw, imported tuna are computed using declared value reported by importers to the Bureau of Census and import volume compiled by Statistics and Market News Service, NMFS Southwest Region.

Table 5.—U.S. cannery receipts (short tons) of domestically caught raw tuna and direct exports by ocean of origin, 1982-87[1].

	Albacore						Albacore	Skipjack						Skipjack
Ocean	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
E. Atlantic	62						12	27	21					10
W. Atlantic		4		1			1		3	944	2,079	1,825	884	970
E. Pacific	5,099	9,434	13,409	6,021	3,158	2,589	7,424	59,264	40,181	22,359	4,992	7,938	14,845	26,947
W. Pacific	1,866	1,032	587	831	369	1,088	937	42,546	114,931	137,678	96,618	103,049	87,842	98,961
Total	7,027	10,470	13,996	6,853	3,527	3,677	8,374	101,837	155,118	160,981	103,689	112,812	103,571	126,888

	Yellowfin[2]						Yellowfin	Total						Overall
Ocean	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
E. Atlantic	1,087						217	1,176	21					239
W. Atlantic	115	70	1,550	4,185	839	60	1,352	115	77	2,494	6,265	2,664	944	2,323
E. Pacific	96,640	65,836	60,753	101,897	103,402	106,330	85,711	161,003	115,478	96,521	112,910	114,498	123,734	120,082
W. Pacific	24,290	54,701	49,777	31,982	40,359	70,291	40,222	68,702	170,646	188,042	129,431	143,777	159,221	140,120
Total	122,132	120,634	112,080	138,064	144,600	176,651	127,502	230,996	286,222	287,057	248,606	260,939	283,899	262,764

[1] Includes tuna destined for canning; excludes tuna destined for the fresh market; includes tuna landed directly or transshipped to a foreign country; excludes tuna exported from the U.S. east and wests coasts.

[2] Includes bigeye, blackfin, and bluefin tunas.

Table 6.—U.S. cannery receipts (short tons) of imported raw tuna by ocean of origin, 1982-87[1].

	Albacore						Albacore	Skipjack						Skipjack
Ocean	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
E. Atlantic	19,815	16,935	27,392	30,655	35,475	35,543	26,054	34,358	35,882	10,828	19,713	39,499	17,700	30,040
W. Atlantic	21,129	16,127	17,209	25,486	36,631	21,827	23,316	18,070	9,059	20,650	15,434	14,731	5,000	16,066
E. Pacific	48	243	439			145	146	4,501	9,245	17,146	15,733	10,443	14,418	11,708
W. Pacific	35,374	23,226	32,340	28,667	28,916	26,948	29,705	72,742	72,699	30,427	24,604	63,001	29,059	48,898
Indian	18,232	16,324	15,464	10,344	11,27	16,898	14,327	5,637	7,988	13,581	29,547	8,094	28,881	12,460
Total	94,598	72,855	92,844	95,152	112,292	101,361	93,548	135,308	134,873	92,632	105,031	135,768	95,058	119,172

	Yellowfin[2]						Yellowfin	Total						Overall
Ocean	1982	1983	1984	1985	1986	1987	1982-86 avg.	1982	1983	1984	1985	1986	1987	1982-86 avg.
E. Atlantic	9,320	4,618	3,258	5,075	5,949	5,403	5,644	55,911	66,532	46,558	61,137	70,246	58,646	61,738
W. Atlantic	3,058	6,446	3,259	10,910	5,507	3,201	5,836	40,643	29,527	57,046	57,572	39,875	30,028	45,218
E. Pacific	19,200	7,492	9,222	29,572	46,945	48,180	22,486	12,236	18,906	46,718	62,678	26,898	62,743	34,340
W. Pacific	18,800	18,814	23,799	15,262	14,380	19,291	18,211	114,782	128,838	74,356	67,900	119,253	75,298	96,814
Indian	835	962	2,192	6,542	6,354	6,274	3,377	22,923	25,644	30,467	47,171	24,490	52,053	30,164
Total	51,213	38,332	41,730	67,361	79,135	82,349	55,554	246,495	269,447	255,145	296,458	280,762	278,768	268,274

[1] Includes inported tuna destined for canning; excludes tuna destined for the fresh tuna market or designated as flakes and not fit for human consumption.

[2] Includes bigeye, blackfin, and bluefin tunas.

All albacore received from the Atlantic and Indian Oceans consisted of imports. Receipts of albacore from the Atlantic Ocean decreased 20 percent from 1986, receipts from the Pacific decreased 5 percent, and those from the Indian Ocean increased 50 percent (Table 5, 6).

With the exception of the record 1986 pack, the 1987 U.S. pack of white meat tuna, 7.2 million standard cases, was the largest since 1978; the 1987 pack was 11 percent less than the record 1986 pack (Fig. 5, Table 7)[8].

During 1987, wholesale list prices for U.S.-produced nationally advertised brands of white meat tuna ranged between $55.40 and $63.57 per standard case. With discounts, wholesale prices fell below $49.00 a standard case. Whole-

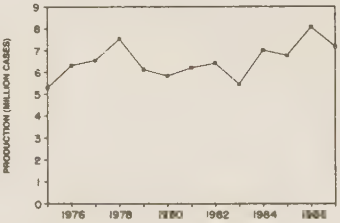

Figure 5.—U.S. production of canned white meat tuna, 1975-87.

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[8] A standard case consists of 48 6.5-ounce cans of 19.5 pounds.

Table 7.—Addtions to the U.S. supply of canned tuna, volume and value, by source and form, 1975-87.

Year	Domestic White	Domestic Light	Imported	Total
	Volume (1,000 standard cases[1])			
1975	5,296	21,854	2,650	29,800
1976	6,312	24,416	3,020	33,748
1977	6,559	21,544	1,776	29,879
1978	7,528	28,615	2,655	38,798
1979	6,129	25,678	2,754	34,561
1980	5,825	25,049	3,259	34,133
1981	6,204	25,948	3,633	35,785
1982	6,416	21,199	4,491	32,106
1983	5,444	24,844	6,273	36,561
1984	7,012	24,489	8,324	39,825
1985	6,764	21,185	10,972	38,921
1986	8,069	24,589	12,134	44,792
1987	7,174	26,364	10,856	44,394
	Value (U.S. dollars)			
1975	136,678	515,957	45,951	698,586
1976	212,869	640,594	67,502	920,965
1977	240,734	665,880	44,658	951,272
1978	296,506	976,754	63,822	1,337,082
1979	243,851	859,998	65,071	1,168,920
1980	252,290	891,237	97,254	1,240,781
1981	294,292	885,846	110,359	1,290,497
1982	275,400	643,046	113,346	1,031,792
1983	197,011	661,586	137,324	995,921
1984	255,997	616,280	167,268	1,039,545
1985	269,887	550,882	209,138	1,029,907
1986	320,795	560,723	227,919	1,109,437
1987	313,611	704,048	206,920	1,224,579

[1]Standard case = 48 6.5-ounce cans.
Sources for domestic data: U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv. 1976-87. Fisheries of the United States, 1976-1987. Curr. Fish. Stat. 6900, 7200, 7500, 7800, 8000, 8100, 8200, 8300, 8320, 8360, 8385, 8700, var. pagin. Also, U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv. 1975-85. Canned Fishery Products, 1975-1984. Curr. Fish. Stat. 6701, 6901, 7201, 7501, 7801, 8001, 8101, 8201, 8301, 8319, 8359, var. pagin.
Sources for import data: U.S. Dep. Commer., Bur. Census computerized data files, 1974-87.

sale prices for private brands ranged between $43.50 and $51.50.

The value of the U.S. white meat pack was $314 million (FOB plant value) in 1987, down 2 percent from 1986 (Table 7). Dividing value by production yields a weighted average price of $43.71 per standard case in 1987, an increase of 10 percent over the average value in 1986.

Light Meat Tuna

In the United States, tuna with flesh color lighter than Munsell value 5.3 may be canned as light meat tuna[9]. Seventy-nine percent of the U.S. pack in 1987 was light meat tuna. The 6.5-ounce can of chunk style, light meat tuna in water has for several years been the most popular tuna product consumed in the United States.

Production by the U.S. Tropical Tuna Fleet

The U.S.-flag, tropical tuna fleet began fishing in the early 1900's off the coast of California (Greenough and Joseph, 1986; Joseph[10]). In the early years, the fleet consisted entirely of baitboats (pole and line gear). Beginning in the mid-1950's, larger baitboats were converted to purse seine, which in the 1960's became the dominant gear. During the mid-1960's to mid-1970's the fleet expanded rapidly as new and larger purse seiners were constructed. The baitboat fishery was concentrated in coastal areas and near offshore islands near supplies of baitfish. As purse seining became the dominant gear, the fleet expanded its operations to offshore regions of the eastern Pacific, to the Atlantic in some years, and in the late 1970's and particularly after 1982, to the western Pacific.

At the beginning of 1987, the U.S.-flag, tropical tuna fleet consisted of 85 vessels with an overall carrying capacity of 88,252 tons: 80 purse seiners and 5 baitboats. By the end of 1987, the fleet had declined to 83 vessels (76 purse seiners and 7 baitboats) with a total carrying capacity of 81,279 tons. Nine of the 83 vessels were inactive.

During 1987, the U.S. tuna fleet operated exclusively in the Pacific Ocean. There were 34 vessels active in the western Pacific during the first quarter with a combined carrying capacity of 41,255 tons. By the end of the year the number in the western Pacific had declined to 29 vessels with a capacity of 35,875 tons, a 15 percent decrease in number and a 13 percent decrease in capacity. Thirty-five vessels with a total carrying capacity of 33,263 tons operated in the eastern Pacific during the first quarter, increasing to 45 vessels with a capacity of 37,829 tons by the end of the year, a 22 percent increase in number and 12 percent increase in capacity.

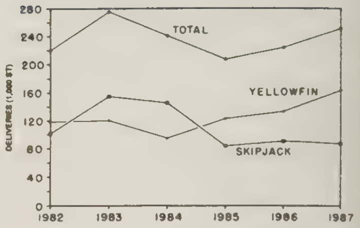

Figure 6.—Deliveries of light meat tuna to U.S. canneries by U.S. fishermen by species, 1982-1987.

Receipts of domestically caught, light meat tuna at U.S. canneries in 1987, 251,100 tons, were the highest since 1983, 12 percent above the 1986 receipts and 8 percent above recent average receipts (Fig. 6, Table 1). As in 1985 and 1986, receipts of yellowfin tuna exceeded skipjack receipts, comprising 65 percent of the total. Yellowfin receipts (includes small amounts of bigeye, bluefin and blackfin tuna) increased 23 percent over 1986 receipts while skipjack receipts decreased 4 percent.

Sixty-three percent of domestic deliveries to U.S. canneries were to American Samoa and California canneries and 37 percent went to Puerto Rico canneries[11]. Receipts at American Samoa and California in 1987 were 158,734 tons, up 23 percent from 1986 receipts. Receipts at Puerto Rico were 92,366 tons, down 3 percent from 1986.

In addition to receipts at U.S. canneries, U.S.-flag vessels exported 16,256 tons of skipjack tuna and 12,866 tons of yellowfin tuna to foreign canneries in 1987, down 27 percent for skipjack and up 12 percent for yellowfin from 1986.

Owing to increased worldwide demand for raw tuna, contract ex-vessel prices for frozen light meat tuna increased dramatically in 1987 (e.g., up 47 percent for yellowfin tuna >20 lb.) (Fig. 7). In January, contract ex-vessel prices (without quality adjustments) for frozen light

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[9] The U.S. Food and Drug Administration lists the following as species that may be canned as light meat tuna: *Thunnus thynnus* (also *T. orientalis*), northern bluefin tuna; *T. maccoyii*, southern bluefin tuna; *T. alalunga*, albacore; *T. atlanticus*, blackfin tuna; *T. obesus*, bigeye tuna; *T. albacares*, yellowfin tuna; *T. tonggol*, longtail tuna; *Katsuwonus pelamis*, skipjack tuna; *Euthynnus affinis*, kawakawa; *E. alletteratus*, little tunny; *E. lineatus*, black skipjack. (U.S. Gov. Print. Off. 1985. 21 Code Fed. Reg. Sect. 161.190 (a) (2)).

[10] Joseph, J. 1988. A review of the fishery for tropical tunas in the eastern Pacific Ocean. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Reg./Southwest Fish. Cent., Tuna Newsl. (90):5-7.

[11] The majority of landings in the category American Samoa/California are in American Samoa. The category is used to maintain confidentiality.

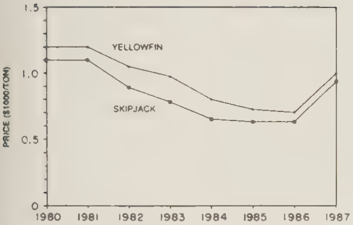

Figure 7.—Contract price for representative size skipjack (4-7.5 lb) and yellowfin (7.5-20 lb) tuna paid by U.S. canneries to U.S. fishermen at the end of the year, 1980-87.

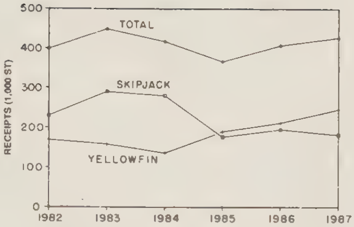

Figure 8.—Receipts of light meat tuna by U.S. canneries by species, 1982-1987.

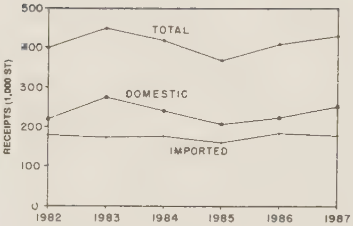

Figure 9.—Receipts of light meat tuna by U.S. canneries by source, 1982-87.

meat tuna in all species and size categories were at a low level (Table 2). Contract prices rose through July then held steady through the remainder of the year. Vessels which chose to sail without contracts were able to command premiums of $20-40 per ton or more above contract prices. For a short period in the fall of 1987, premiums reached a high as $300 per ton[12].

Total ex-vessel revenue from the sale of U.S.-caught light meat tuna was about $208.6 million in 1987, 35 percent greater than in 1986. The ex-vessel value of domestically caught skipjack tuna delivered to U.S. canneries was $62.5 million, up 12 percent from 1986. The average ex-vessel price (total revenue divided by total domestic receipts) was $716 per ton, a 16 percent increase from 1986 (Table 4). The ex-vessel value of domestically caught receipts of yellowfin tuna was $146.1 million in 1987, 48 percent above 1986. The average ex-vessel price for yellowfin tuna in 1987 was $892 per ton, an increase of 20 percent from 1986.

U.S. Processing of Canned Light Meat Tuna

Total receipts (U.S.-caught plus imports) of raw light meat tuna at U.S. canneries in 1987 (428,507 tons) were at their highest levels since 1983, up 5 percent from both 1986 and recent (1982-86) average receipts (Fig. 8, Table 1). Fifty-three percent of total deliveries were to canneries in Puerto Rico, the rest to canneries in American Samoa and California. Receipts at Puerto Rican canneries were 8 percent less than in 1986. Receipts at American Samoa and California canneries were 25 percent more than in 1986.

As in 1985 and 1986, receipts of yellowfin exceeded receipts of skipjack in 1987 (Fig. 8), and 57 percent of raw tuna deliveries consisted of yellowfin, the rest of skipjack. Receipts of domestically caught raw light meat tuna at U.S. canneries in 1987 continued to exceed imports (Fig. 9). Imports, 177,407 tons, made up 41 percent of total raw light meat receipts in 1987 vs. 45 percent in 1986 (Table 1).

Puerto Rico was the major receiving site for imports of raw light meat tuna during 1987, accounting for 77 percent of the total tonnage, compared with 83 percent in 1986 (Table 1). Skipjack tuna made up 54 percent of the 1987 light meat imports, yellowfin the balance. Overall, skipjack tuna imports were down 9 percent from 1986, while yellowfin imports increased 4 percent.

The principal transshipping point for raw light meat tuna imported to the United States in 1987 was the Seychelles, the base of the French and Spanish purse seine fleets operating in the Indian Ocean (Table 4). Of total imports, 16 percent or 27,508 tons was transshipped from the Seychelles. South Korea was the second most important transshipping point, followed by the Ivory Coast. Transshipments of raw light meat tuna from the Seychelles to the United States began in 1983. Since then, Seychelles transshipments have grown and dominated U.S. imports in 1986 and 1987.

Mexico exported 19,405 tons of light meat tuna (does not include non-Mexican caught, transshipped fish) to the United States in 1987, the first full year after the U.S. embargo on imports of Mexican-caught tuna and tuna products ended. When the embargo was lifted, Mexico agreed to voluntarily limit its exports of tuna products to the United States for 3 years, beginning 1 September 1986. At the end of the first agreement year, 31 August 1987, Mexican exports to the United States totaled 16,600 tons, less than the agreed total of 19,200 tons. The agreement calls for limits of 24,000 tons and 30,300 tons in the second and third years, respectively.

The total value of raw light meat tuna imports in 1987 was $135.2 million, down 10 percent from 1986. Skipjack imports were valued at $64.6 million, a decrease of 19 percent from 1986. Yellowfin imports were valued at $70.6 million, the same as in 1986. The weighted average price of imported skipjack tuna was $679 per ton, a decrease of 11 percent from the 1986 price. The price of imported yellowfin funa was $857 per ton, a 5 percent decrease.

The Pacific Ocean continued to be the primary source of all light meat cannery receipts and U.S. direct exports of light meat tuna in 1987, followed by the Atlantic and Indian Oceans (Fig. 10). Total receipts and direct exports were 457,629 tons, of which the Pacific provided 85 percent (Tables 5, 6).

On a regional basis, the western Pacific was the leading production area for U.S. cannery receipts plus direct exports of light meat tuna, with 206,483 tons. Of

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[12] Tim McCarthy, Executive Vice President and General Manager, Bumble Bee Seafoods, Inc., P.O. Box 23508, San Diego, CA 92123. Personal commun., Jan. 1989.

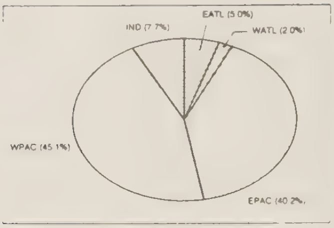

Figure 10.—U.S. cannery receipts and direct exports of light meat tuna by ocean of origin, 1982-87. (Legend abbreviations as in Fig. 5.)

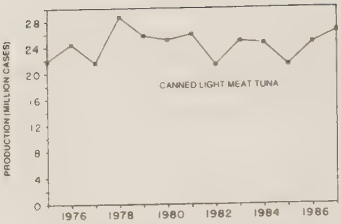

Figure 11.—U.S. production of canned light meat tuna, 1975-87.

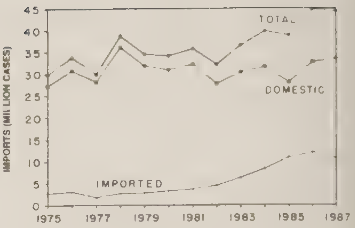

Figure 12.—Additions to the U.S. supply of canned tuna by source, 1975-87.

this total, 77 percent (158,133 tons) was domestically caught and the remainder imported. Skipjack tuna was the predominant species in western Pacific receipts and exports (57 percent of the total). Other oceanic regions contributing, in order of importance, were the eastern Pacific (primarily domestically caught yellowfin tuna), the Indian Ocean (primarily skipjack imports), the eastern Atlantic, and the western Atlantic.

In 1987, the U.S. pack of canned light meat tuna was at its highest level since 1978 (Fig. 11). The pack was 26.4 million standard cases, up 7 percent from 1986 (Table 7).

The wholesale list price of U.S. produced, advertised-label, light meat tuna ranged between $34.20 and $45.00 a standard case, but with discounts the price fell as low as $26.00 a case during the year. Wholesale list prices for private-label light meat tuna ranged between $23.00 and $31.50.

Total production of canned light meat tuna, both name- and private-label brands, was valued at $704 million (FOB plant value) in 1987, up 26 percent from 1986. The weighted average price was $26.70 per standard case, an increase of 17 percent from 1986.

U.S. Imports of Canned Tuna

The United States imported 10.8 million standard cases (105,800 tons) of canned tuna in 1987 (Table 7). Imports actually declined in 1987, the first reversal of the spectacular increase in imports (a compound annual increase of 17 percent) which began in 1978 (Fig. 12). Imports in 1987 decreased 11 percent from 1986 (Table 7).

Foreign-processed canned tuna is subject to an import tariff. Tuna canned in oil is subject to a 35 percent ad valorem tariff. Tuna canned not in oil is subject to a tariff rate quota which allows imports of up to 20 percent of the previous year's domestic production to enter at 6 percent ad valorem. Imports in excess of the quota level enter at 12.5 percent ad valorem. The 1987 quota was 45,750 tons (4.7 million standard cases).

An indication of the rates of imports is the date on which the quota is reached. In 1987, the quota was reached on April 4, the earliest closure date since the quota program began.

The majority (86 percent) of canned imports were of light meat tuna (in water) at 9.4 million standard cases (91,000 tons). White meat tuna in water contributed 13 percent at 1.4 million cases (14,700 tons). One percent of 1987 canned imports were of tuna canned in oil. Due to the high tariff, U.S. imports of tuna packed in oil have never been large and in 1987, 16,800 standard cases (164 tons) were imported.

Thailand, Taiwan, the Philippines, and Japan were the major exporters of canned tuna to the United States in 1987, as they have been since 1982 (Table 8). Thailand was the leader, shipping 73,400 tons (7.5 million standard cases), 70 percent of total 1987 U.S. imports.

The value of imported, canned tuna in 1987 was $207 million (FOB plant value not including duty) (Table 8). The weighted average price of imports was $1,940 per ton or $18.87 per standard case, the same as in 1986.

U.S. Consumption of Canned Tuna

Per capita consumption of canned tuna products in the United States for 1987 (excluding noncivilian consumption) was 3.5 pounds, 3 percent less than in 1986. According to industry reports, 78 percent of 1987 U.S. canned tuna consumption was of light meat tuna and 22 percent was of white meat. Based on these proportions, per capita consumption of white meat was 0.77 pounds (1.9 standard cans), 1 percent less than in 1986. Per capita consumption of light meat tuna in 1987 was 2.73 pounds or 6.7 standard cans, 4 percent less than in 1986.

The retail composite canned tuna price (an average weighted by volume of product type) was $2.26 per pound in 1987, unchanged from 1986. The composite price for canned white meat tuna was $3.21 per pound; the price for light meat tuna was $1.99 per pound. Based on per capita consumption, 1987 U.S. per capita expenditure for canned tuna was $7.91, $2.47 for white meat tuna and $5.44 for light meat tuna.

Discussion

Generally, 1987 was a good year for the U.S. tuna industry. Domestic cannery receipts and production were up, as were ex-vessel and wholesale prices. U.S. landings of light meat tuna were up in 1987, while foreign catches, particularly from the Atlantic and Indian Oceans, were down, creating tight supplies in a strong global market and, as a result,

Table 8.—U.S. imports of canned tuna (oil and water), by principal sources, 1982-1987.

	Quantity (1,000 pounds)						Value (U.S. $1,000)					
Source	1982	1983	1984	1985	1986	1987	1982	1983	1984	1985	1986	1987
Canada	2	2,106		88	9	83	5	2,986		75	7	63
Ecuador			890	5,175	2,886	5,112			837	4,676	2,603	4,481
Indonesia	595	2,634	2,222	1,388	815	1,505	699	2,679	2,102	1,186	690	1,248
Japan	25,481	20,387	26,855	23,703	10,558	4,688	38,561	24,643	29,186	28,142	14,755	7,375
Malaysia	755	3,083	1,608	3,878	2,401	1,573	1,242	4,068	1,893	4,498	3,160	1,985
Philippines	27,631	32,018	22,225	30,797	27,982	20,858	31,085	32,291	20,396	25,930	23,124	16,576
South Korea	49	68	82	58	1,443	306	79	69	75	58	1,230	267
Spain[1]	120	133	214	336	237	198	300	268	376	560	557	588
Taiwan	10,704	18,710	17,935	23,472	28,579	25,924	14,366	22,772	22,475	29,801	34,483	34,809
Thailand	18,667	39,930	89,685	122,666	152,297	146,928	22,711	43,259	89,253	111,852	139,561	135,368
Other	2,575	3,260	597	2,387	9,414	4,510	4,299	4,289	677	2,360	8,456	4,160
Total	86,479	122,329	162,313	213,948	236,621	211,685	113,347	137,324	167,270	209,138	228,626	206,920

[1] Mainly oil packed.

Sources: U.S. Dep. Commer., Bur. Census computerized data files, 1982-1987.

higher ex-vessel prices. With the increase in landings and ex-vessel prices, earnings by the U.S. fleet increased significantly.

While eastern Pacific fishing grounds continue to be of key importance to the U.S. purse seine fleet fishing for tropical light meat tunas, the importance of western Pacific grounds increased as access became more assured with the signing, in 1987, of an agreement between the United States and South Pacific nations allowing U.S. vessels access to South Pacific fishing zones. The agreement was precipitated by jurisdictional claims by many Pacific island states over tuna in 200-n.mi. extended economic zones (EEZ's) and problems caused when, in the early 1980's, several U.S. vessels were seized for fishing in claimed island exclusive fishing zones. Seizures triggered relaliatory U.S. embargoes on imports of tuna products from the seizing nations as provided for by the Magnuson Fishery Conservation and Management Act.

To resolve these problems, the United States and 16 Pacific island states negotiated a regional licensing arrangement, signing a treaty formalizing the arrangement in 1987. Terms of the treaty grant U.S. vessels fishing rights within fishing zones of a large region of the South Pacific Ocean and provide for license fees and technical and economic assistance to the South Pacific states. Negotiations leading to a treaty arrangement allowing for U.S. access to EEZ's of Central and South American nations and for collective management of eastern Pacific tuna resources continued in 1987 but have yet to yield an agreement.

A bright spot for U.S. tuna fishermen was the devleoping South Pacific albacore fishery. In the face of continuing declines in landings by the U.S. albacore fleet from its traditional west coast grounds, efforts to develop new grounds in the South Pacific began in 1986. Initial fishing success and high demand for albacore prompted U.S. jigboats to develop the southern fishery. Between January and April, 1987, seven U.S. jigboats operated in the central South Pacific catching 840 tons of albacore. Catches were landed in Tahiti and sold at an average price of $1,300 per ton.

Worldwide, the demand for canned tuna, and hence raw tuna, was up in 1987 while harvests in some areas were down. This contributed to increases in ex-vessel and wholesale prices. The European tuna industry, being much more vulnerable to the shortfall in raw tuna production from the Atlantic and Indian Oceans, was unable to satisfy increasing European demand for canned tuna, and in 1987 much of the foreign processed canned tuna, as well as foreign caught raw tuna, entered European rather than U.S. markets. U.S. imports of canned tuna were down 11 percent from 1986 levels, the first time in recent years than imports have declined.

U.S. processors took advantage of the 1987 global tuna situation and increased their share of the domestic canned tuna market, and U.S. cannery production rose. Nonetheless, with the decline in imports, the total amount of canned tuna available to U.S. consumers fell 1 percent from 1986. Since U.S. canned tuna consumption was down slightly in 1987, the overall decrease in supply would help explain the improvement in wholesale canned tuna prices, and an unchanged composite retail price from 1986.

Acknowledgments

This review would have been impossible without the support of the U.S. tuna canning industry, officials of which continue to voluntarily report data on industry activities—we appreciate their support. We acknowledge the assistance of Diane Pickelsimer, Henry Orr, and Lorraine Prescott, NMFS Southwest Fisheries Center; and Richard Deering, NMFS Southwest Regional Office in preparing this report. We thank the many colleagues, and particularly members of the tuna industry, for their careful review of the manuscript.

Literature Cited

Greenough, J. W., and J. Joseph. 1986. International management of the highly migratory tunas and billfishes. *In* K. A. Hinman (coordinator) and R. H. Stroud (editor), Multi-jurisdictional management of marine fisheries. Proc. Eleventh Annu. Mar. Rec. Fish. Symp., Tampa, Fla., May 1-2, 1986, p. 121-138. Natl. Coalition Mar. Conserv., Inc., Savannah, Ga.

Herrick, S. F. 1984. U.S. tuna trade summary, 1982. Mar. Fish. Rev. 46(1):1-6.

________ and S. J. Koplin. 1984. U.S. tuna trade summary, 1983. Mar. Fish. Rev. 46(4):65-72.

________ and ________ . 1986. U.S. tuna trade summary, 1984. Mar. Fish. Rev. 48:(3): 28-37.

________ and ________ . 1987. U.S. tuna trade summary, 1985. Mar. Fish. Rev. 49(3): 73-84.

Majors, A. P. 1987. United States North Pacific albacore fishery, 1961-1980. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., NOAA Tech. Memo. NMFS-SWFC-73, 387 p.

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Annex H
Report of the Sub-Committee on Small Cetaceans

Members: Perrin (Convenor), Aguilar, Andersen, Arnason, Asper, Baird, Barlow, Bjørge, Bloch, Braham, Brownell, Buckland, Cawthorn, Christensen, da Silva, DeMaster, Desportes, Donovan, Ford, Fujise, Gunnlaugsson, Hall, Heyning, Hiroyama, Hohn, Inagaki, Jean-Caurant, Johnson, Joyce, Kasamatsu, Kasuya, Kato, Kock, Lens, Lockyer, Lyrholm, Martin, Mate, Michaelis, Moore, Nakamura, Odell, Øien, Reilly, Sanpera, Scott, Sigurjónsson, Smith, Stoker, Swartz, Vikingsson.

1. ELECTION OF CHAIRMAN

Perrin was elected Chairman.

2. APPOINTMENT OF RAPPORTEURS

Martin, Smith, Buckland and Heyning assisted the Chairman as rapporteurs.

3. ADOPTION OF AGENDA

The adopted agenda is given in Appendix 1.

4. REVIEW OF AVAILABLE DOCUMENTS

The following documents contained information relevant to the work of the sub-committee: SC/41/SM1–33; O 4, 5, 7, 12, 17, 20, 22, 25, 26, 27, 33; SHMi14 and 17; SC/40/O 30 Revised; and the national Progress Reports. Sigurjónsson generously distributed to the members of the sub-committee copies of the proceedings volume for the 1987 Workshop on North Atlantic Killer Whales in Provincetown, Massachusetts (Sigurjónsson and Leatherwood, 1988).

5. REVIEW OF EXPLOITED POPULATIONS OF PILOT WHALES

5.1 North Atlantic populations of *Globicephala melas*

The sub-committee reviewed information on North Atlantic pilot whales in 1987 (*Rep. int. Whal. Commn* 38:117–9) and noted a number of areas where substantial information was being developed. The sub-committee discussions this year focused on several of these areas, especially on information derived from recent extensive sampling of the Faroese drive fishery.

The sub-committee wishes to recognise the very great effort and cooperation that have made the international research programme in the Faroes possible and productive and wishes to thank the participants in the programme for the large number of papers and progress reports submitted here.

5.1.1 Stock identity

The long-finned pilot whale is widely distributed in the North Atlantic: in the Central Atlantic (Brown, 1961), from Cape Hatteras north on the western side and on the eastern side from Northwest Africa north to Greenland (SC/41/SM5 and 10). Little information is available on the degree of exchange of animals in different regions of the Atlantic. SC/41/SM28 describes different parasite fauna composition between animals from the Faroe Islands, the eastern North Atlantic near France and the western Mediterranean and notes that a different parasite composition had been described for whales from the earlier Newfoundland pilot whale fishery (Sergeant, 1962). It was noted that the overall degree of parasite infection increased with age and was higher for males. However, the differences that were noted between regions could occur due to diet differences and were not thought to be necessarily an indication of genetic separation. On the other hand, the permanence of scars caused by particular species of nematodes, and the fact that cysts of the type encountered for some cestodes persist for the life of the whale (which is only an intermediate host) suggest that individual pilot whales do not routinely move between the three regions studied or between Newfoundland and eastern Atlantic waters.

SC/41/SM17 examined differences between pods driven in the Faroese fishery using starch-gel electrophoresis on three polymorphic enzymes. An earlier paper (Andersen, 1988) demonstrated a difference between one pod captured at a northern locality and six others taken elsewhere, prompting speculation of the existence of more than one stock. The larger sample now available demonstrates considerable variation between pods, with no obvious geographical or seasonal pattern, and the sub-committee concluded that there is currently insufficient evidence to demonstrate the existence of more than one stock in the area. It was **recommended** that comparison be made between this and other regions in the North Atlantic in order to put into context the degree of genetic variability found in the Faroese catch.

Statistically significant differences in cadmium levels between pods have been found in a study of heavy-metal contamination (SC/41/SM21).

The sub-committee concluded that no new information on stock structure had been obtained to date using the new genetic analytical procedures discussed at the 1987 meeting (various analyses of DNA). However, the sub-committee noted that samples of tissues from pilot whales killed in a western Atlantic mackerel fishery are potentially available (pers. comm. to Heyning from James G. Mead, Smithsonian Institution, during the meeting) and that these could be compared with samples from the Faroese to examine genetic relatedness between whales from the two sides of the Atlantic.

5.1.2 Abundance

There are insufficient data to estimate the number of long-finned pilot whales in the entire North Atlantic. There is no systematic survey information available seaward from the US continental shelf across the central North Atlantic south of 60°N or from the continental shelf of North America between roughly 43°N and 60°N. However, there are data in different regions that can be used to provide some information on abundance. These are described below for three regions: the eastern North Atlantic, the western North Atlantic and the central North Atlantic.

Eastern North Atlantic

Prior to 1987, only limited surveys had been conducted, off Norway, off Iceland, and off Spain (SC/41/SM10). These were designed to study several species of whales, and their main usefulness for pilot whales has been in delimiting overall distribution. The 1987 North Atlantic Survey (NASS-87) provided substantially more information on abundance, over a much larger area (SC/41/SM10). Additional information has also been made available from sightings made aboard Icelandic whaling vessels from 1979 to 1988 (SC/41/O 22).

The Icelandic sightings suggest that pilot whales occur on the western side of Iceland consistently each summer and that the animals appear to be concentrated off southwestern Iceland in the early summer and northwest of the island later in the summer. The data appear reliable for this level of interpretation but are not useful for estimating absolute abundance. The data suggest that whales are not generally found very near the coast, but SC/41/SM26 notes that they occur near the shore occasionally, possibly in conjunction with irregular migration of squid into shallow waters.

Estimates of abundance are presented in SC/41/SM10 for the combined 1987 North Atlantic Sighting Survey study area using data from both Icelandic and Faroese survey vessels. The Norwegian part of the survey did not sight any pilot whales; this is useful negative information about spatial distribution. (It should be noted, however, that pilot whales are known from the coastal waters of Norway to roughly 70°N (SC/41/O 5 and Jonsgard, 1977)). Spain reported 11 sightings, of 123 whales (SC/39/SM14). Pilot whales were seen off West Greenland during the same period (see *Western North Atlantic* below).

For the area covered by the Faroese vessel the estimate of abundance is 72,000 whales (CV 0.4). The main objective for this vessel was to survey pilot whales, and it closed on all but one school. For the Icelandic vessels the abundance estimate is given in two parts, one of 18,950 (CV 0.5) for sightings which the vessel closed on, and the second of 12,945 (CV 0.25) for sightings which the vessel did not close on. All estimates were based on the assumption that $g(0)=1$. Further, the estimates only relate to the surveyed areas; this corresponds to only part of the range of the species in the Northeast Atlantic. Because the primary objective for the Icelandic vessels was to survey fin and minke whales, the decision to close or not to close on pilot whale sightings was made as the survey proceeded; the authors of the paper felt that the decision process was such that larger schools were more likely to be closed on. These two estimates were obtained by treating the sightings made under the two protocols as if they were of two different species.

A number of factors were identified in SC/41/SM10 that need to be considered as potential analytical problems. These include (1) low observer eye-level height aboard the Faroese vessel, (2) the diffuse nature of some of the pilot whale schools, where the initial sighting frequently was of a component of a school, (3) different levels of experience of the observers with respect to estimating school size for this species, and (4) uncertainty in how to account for diving animals. It was also noted that the smaller average sighting distances for the Faroese vessel were on the order of the apparent diameter of the spread-out schools, making estimating distance of the school from the trackline when sighted problematical for some schools. However, this problem had been addressed in part by truncating the data to eliminate the largest schools, which tend to be spread out, in the analysis. It was noted that this may tend to bias the estimate downward.

The sub-committee agreed that these factors, especially that of the form of schools (which might introduce a positive bias) and the difficulties in estimating total school size because of diving behaviour (which would introduce a negative bias), were of concern. Additional concerns were raised about the treatment of the Icelandic data separately for passing and closing mode. Several alternative analytic approaches should be explored, for example by using hazard-rate estimation procedures or by ignoring the closing versus passing mode issue and stratifying by school size. The authors felt that this would not change the results significantly, as distance from the trackline shows no relationship with school size in the data. Given the above concerns it is clear that the passing mode estimate is biased downward, and it is not obvious how to combine the two estimates for the Icelandic vessels.

The sub-committee noted that there was greater uncertainty in the estimate than indicated by the calculated CVs because of the effects of the above-described factors; however, it is not possible to determine if the several estimates are likely biased upward or downward. The sub-committee believes that it would be useful to include all relevant details of the surveys and analyses in the paper rather than referring to information reported elsewhere, i.e. in SC/41/O 30 and SC/40/O 30 Revised. It would also be useful to include a map showing the actual tracklines and the division of effort into passing and closing modes. Data on size estimates of schools at the Faroes *before* they are driven would also be useful in evaluating the survey school size estimates.

Additionally, the sub-committee **recommended** that the survey area should be extended in the future to better determine the area occupied during the survey period, that information from radio telemetry on dive times (such as collected by Mate, 1988) might be used to improve estimates of school size, and that detailed behavioural studies of school conformation be done to better understand the applicability of line-transect theory to pilot whales.

Western North Atlantic

Mercer (1975) estimated the abundance of pilot whales in the Newfoundland area to have been 60,000 animals in 1947, based on cumulative catches after WWII. Pilot whale abundance in the Newfoundland area was thought to have been greatly reduced by the early 1960s by a directed fishery. A single aerial survey conducted in 1980 off Newfoundland and Labrador (Hay, 1982) yielded an estimated abundance of 6,700 to 19,600 pilot whales. A series of aerial surveys have been conducted off Greenland in 1984, 1985, 1987 and 1988 (SC/41/O 17); these noted the presence of pilot whales in similar areas in two of the four years. Both surveys have provided information on distribution along the coastal regions on both sides of Labrador Strait, but the stock relationships between animals on the Canadian and Greenland sides are unknown.

A series of systematic sighting surveys were conducted off the northeastern USA from 1978 using airplanes and from 1980 to the present using fishery research vessels (SC/41/SM18; Smith, Payne, Heinemann, Waring and Longe, 1988). The aerial sighting surveys have been used for estimating abundance, with estimates in the range of 10,000 to 12,000 pilot whales. Insufficient information was available to allow review of these estimates by the sub-committee. For example, estimates of variance were not given. The sighting surveys aboard the fishery research vessels were conducted during transits between sampling stations. The sampling design of the fishery surveys includes both stratified-random and fixed sampling stations. Densities of animals for the several geographic strata are shown to vary seasonally, with increases in the summer and fall in the northern part of the study areas and along the shelf edge.

The density estimates are derived using line transect methods, but the methods of the analyses are not given in sufficient detail. The estimates were expanded to estimates of total abundance within the study area; these range seasonally from roughly 4,000 to 10,000 pilot whales. Estimates of variability of the estimates are not given; this prevented the sub-committee from assessing their validity.

A difficult problem faced by the survey analysis is separating sightings for the two species of pilot whale inhabiting the region, *G. melas* and *G. macrorhynchus*. Contrary to the assumption made in SC/41/SM18, these are indications that the two species strand with roughly equal frequency in a band of overlap between about 35° and 40°N (pers. comm. to Heyning from J.G. Mead, Smithsonian Institution, during the meeting). The information presented in SC/41/SM18 was not sufficient for determining if the gaps in the winter distribution indicated presence and separation of the two species in the survey area; inclusion of effort data would help with this determination.

The difficulty of identifying the two species of pilot whales at sea and determining their relative distributions were noted and several alternative approaches suggested. These included examination of the skulls and teeth of animals killed incidentally in the mackerel fishery, biochemical or genetic analysis of tissues from animals in the catch or of biopsy samples collected during the surveys, and analysis of recordings of sound production.

These shipboard surveys provide needed information on the distribution of cetaceans in the North Atlantic, and the sub-committee notes with concern that the surveys are now occurring at very reduced frequency. It is suggested that in future surveys the area covered be extended to the east because of the likely occurrence of pilot whales there. Mate reported that the pilot whale that he tracked by satellite moved out of the survey area to the east in waters of over 4,500m.

Central North Atlantic

There are few sighting data for this region beyond those summarised by Brown (1961); none are suitable for estimating abundance. No systematic sighting surveys have been conducted here. The results from the NASS-87 do not reveal a decline in encounter rate along the legs reaching southwest from the Faroe Islands, and the US surveys suggest no decline in sightings eastward across the study area, suggesting that the distribution of pilot whales continues into at least certain parts of the central North Atlantic. Further, Smith reported that G. Waring of the Northwest Fisheries Center at Woods Hole, Massachusetts, has data on several sightings of pilot whales by US observers aboard Japanese longline vessels in the region of the Gulf Stream.

5.1.3 Migration

There is very little direct information on migrations. There is a suggestion of an increase of abundance in Icelandic waters in the early summer, with numbers peaking between July and September (SC/41/O 22). Pilot whales occur in Faroese waters in all months of the year, and the seasonality of catches, with most animals historically taken in the summer, may now be less evident (SC/41/SM8). Similarly, in British waters pilot whales occur year-round (Evans, 1980; Martin, Reynolds and Richardson, 1987) and there is no recent evidence to support an earlier hypothesis of seasonal offshore-onshore movements. The sightings data in SC/41/SHMi8 (and Smith *et al.*, 1988) provide useful information on seasonal distributional patterns seaward to the edge of the continental shelf, suggesting longshore and inshore-offshore movements. No clear distinction has yet been shown between animals in any two areas of the North Atlantic which could exclude the possibility of latitudinal or longitudinal movements or migration, but neither has any migration been proven. The availability of prey is likely to be a major factor in determining the seasonal movements of pilot whale schools, but recent evidence from the Faroes indicates that pods may still occupy traditional feeding grounds when the normal prey are not available (SC/41/SM13).

The sub-committee agreed that the long-finned pilot whale is a species likely to be particularly suitable for studies of migration and movements using radio and **recommended** that the proposed project using satellite-linked transmitters at the Faroes to study movements, described at this meeting two years ago, be undertaken.

5.1.4 Life history

Age determination

SC/41/SM4 examined in detail the characteristics and rate of deposition of dentinal and cemental layers in pilot whale teeth. The principal conclusion, based on the examination of tetracycline-marked teeth from captive *G. macrorhynchus* of known history, is that one growth-layer group (GLG) is deposited annually in cementum and in dentine until 15–25 years of age. This confirms that the current criteria used to determine age in *Globicephala* spp. are correct. Other features in the teeth, principally anomalous layers and deposits, varied in frequency between pods from different geographical regions and between sexes and age groups. Some anomalies may result from stress and, if so, could be used to indicate major physiological occurrences such as puberty or periods of starvation. The sub-committee received this paper with interest and **recommended** that the incidence of marker lines and other anomalies in teeth be looked at in more detail to determine possible links with oceanographic conditions, food availability and life-history events.

Growth and reproduction

The sex ratio of foetuses in the Faroese catch was examined in SC/41/SM12, using sex chromatin, phenotype and gonadal histology. The sex ratio of the sample did not differ significantly from unity. SC/41/SM14 gives a preliminary report on growth and sex distribution of Faroese pilot whale foetuses. The sex ratio in this sample was 47% males:53% females in foetuses less than 92cm long and 40%:60% in larger foetuses. It was agreed that further analysis is required before the authors' suggestion of a greater length-at-birth in Faroese whales than in those off France and Newfoundland can be accepted.

SC/41/SM11 presents data on the male sexual cycle and age at attainment of sexual maturity in Faroese pilot whales. From an examination of testis weight, histological characters such as spermatogenesis and tubule diameter, and testosterone levels it was concluded that male sexual activity peaks between March and August, but that successful mating could occur throughout the year. In discussion, it was suggested the testosterone levels may be correlated with dominance rather than maturity; the highest levels were found in males less than 30 years old. The sub-committee discussed whether the methods used in this analysis can be equated with those employed by Sergeant (1962) on Newfoundland samples and concluded that comparison between the results for the two areas is difficult.

SC/41/SM15 provides useful new information on age-related parameters. The authors indicated that they will undertake a more complete analysis of these parameters, taking into account comments made by the sub-committee.

Information on two mass strandings of pilot whales on the Icelandic coast is presented in SC/41/SM26. One of the strandings was thought to comprise almost an entire pod, whereas the other was known to represent only part of a larger group of animals. In general, biological parameters are within the range found elsewhere in the Northeast Atlantic. In discussion, it was suggested that the age of sexual maturation given in the paper, based on small sample sizes, should be treated with caution.

Social organisation and breeding system

The results of genetic fingerprinting work on Faroese pods are given in SC/41/SM30. Although the data are as yet preliminary, some very important conclusions can apparently be drawn about the social structure of *G. melas*. Reproductively active adult males move between schools, and do so within a few months of fertilising females in such a school. Faroese pilot whale pods may be considered as matrilines, which male offspring will eventually leave but in which female offspring will probably remain. The mechanism by which males might transfer from one pod to another was discussed by the sub-committee. With little evidence so far of males being encountered individually or in small groups around the Faroes, transfer may be accomplished when two or more pods merge at times of year when aggregations of the species are particularly large. The genetic analyses discussed above under *Stock identity*, using starch-gel electrophoresis of isozymes, gave results in accord with the picture emerging from the DNA fingerprinting work.

Some selected external morphological characteristics, including colour pattern, were examined in the Faroese catch (SC/41/SM9) in an attempt to characterise individual pods, but no differences could be detected between the pods. Variation in length of dorsal fin previously noted turned out to be ascribable to seasonal variation in fatness.

Seasonal change in body condition

SC/41/SM5 reports on the body fat condition of Faroese pilot whales. A marked annual cycle was found in all age and sex classes whereby blubber thickness and thus energy reserves increased during the winter and decreased during the summer, peaking around the probable time of mating activity in spring. A link between the cycle of energy reserve levels and reproductive demands was postulated, but, if this is the case, it is not clear whether reproduction is timed to take advantage of peak food availability or simply more food is eaten when energetic demands due to reproduction are high. The fact that all categories of animals synchronise their deposition of blubber, regardless of reproductive status, indicates that food availability is the more likely driving factor.

Mass die-offs

Information is given in SC/41/O 5 and ProgRep Norway on an unusual apparent die-off of sperm, killer and pilot whales in the North Atlantic. It is speculated in SC/41/O 5 that the bodies may have drifted in the Trans-Atlantic Current from a region off North America where odontocetes and baleen whales have been involved in other recent die-offs, but the estimates of rates of decomposition and current speed upon which this speculation is based need further examination. Further, some of the stranded sperm whales were freshly dead. Other reports of unusual mortality of odontocetes in European waters may be linked to the event reported by Norway. Martin reported that many freshly dead pilot whales were reported to be floating off the northernmost Shetland island by several fishermen in February/March 1989, and Desportes reported (pers. comm. from R. Duguy, Oceanographic Museum of La Rochelle) that about 600 dolphins, mostly *Delphinus delphis* but including striped dolphins and pilot whales, were washed up in western France in late February-March 1989 after a heavy storm. The sub-committee **recommended** that efforts be made to determine the causes of mortality in any new die-offs. These efforts should include examination of the carcasses by veterinarians experienced in marine mammal pathology.

5.1.5 Population dynamics

No paper was presented on this topic, and the sub-committee **recommended** that attention be given to it using the Faroese data. For example, it was suggested that enough frequency-at-age data may now exist to allow construction of life tables for males and females.

5.1.6 Ecology

Feeding habits

Paper SC/41/SM13 considers the evidence on pilot whale feeding derived from examination of stomachs in the Faroese catch. In contrast to a smaller study in 1984, the 1986–88 samples contained no flesh whatsoever, and this coincided with the collapse of the local squid fishery. Squid beaks continued to be found, indicating that squids remained the primary prey group, but pilot whales apparently did not feed in nearshore waters in recent years.

Squid species represented by indigestible remains were mostly pelagic, luminous and shoaling. Variable digestion rates render quantitative assessment of the composition of prey species taken very difficult. In discussion, it was noted that some fish species, such as cod and blue whiting, are very common and abundant in Faroese waters at particular times of the year, yet rarely appear in pilot whale stomachs. Thus, while the type of prey taken may reflect local availability to some extent, some degree of choice is apparently exercised by the whales, especially between squid and fish.

Contaminants

SC/41/SM22 provides information on the levels of DDT and PCBs in Faroese pilot whale tissue. In general, levels were within the range encountered in this and other species elsewhere in the North Atlantic, but significant differences in pollutant loads were found between the two pods examined in this study. Comparison between pilot whales from the Faroes and other areas is complicated because the results available in the literature extend from the mid-1970s to the late 1980s, and environmental pollution is known to have changed during this period. Morever, some samples were based on stranded animals while others were from driven pods. A second paper on synthetic pollutants in Faroese pilot whales, SC/41/SM24, gives results consistent with those in SC/41/SM22, but was based on fewer data and lacked biological information on the sampled whales. In discussion, concern was expressed about the impossibly high relative lipid content reported for many samples, and there was some indication that tissues may have been contaminated by incorrect storage, perhaps in plastic bags.

A study of heavy metals in pilot whale tissues is reported in SC/41/SM21. Cadmium levels were fairly high, and mercury accumulative with age. At this point in the continuing study, variances for mercury are high, so that little can yet be said about differences between pods or among the various age and sex categories of whales, but for cadmium significant difference were found between pods. These results will be investigated further.

Parasites

Parasite burdens of Faroese and other Northeast Atlantic pilot whales are examined in SC/41/SM28. Twenty-one different species were encountered, including three new to science. Cyamids were more common on large males than on other age and sex classes. This may be a result of behavioural differences or because adult males are likely to be more scarred and thus present a potentially greater area for cyamid colonisation. Nematode infestation first became obvious in the second year of life, presumably as a direct result of the increasing proportion of solid food in the diet. Thereafter, quantities of nematodes found in the stomach increased through life, before showing a slight decrease in the oldest individuals. The authors speculated that this may be due to the death of the most heavily parasited older animals. Four parasite species were considered to have significant pathological effects on the host, perhaps causing death in extreme cases. As noted above under *Stock Identity*, it was suggested in discussion that permanent parasites, such as the cestode *Diphyllobothrium*, are likely to be good indicators of animal movements or of segregation between geographical areas on the time scale of at least one whale lifespan.

5.1.7 Exploitation

The now defunct Canadian pilot whale fishery, the Faroese drive fishery and the several fisheries causing incidental mortality (including the USA mackerel fishery – SC/41/SM19 and Waring, Parry, Nicolus, Gerrior and Payne, 1989) have removed a large number of pilot whales from the North Atlantic.

There was no new information available on analysis of the long time series of catch statistics (several hundred years) for the Faroes (SC/38/SM7, 20); 1,690 pilot whales were landed in 1988 (SC/41/ProgRep Faroes).

SC/41/SM19 presents an analysis of the spatial distribution of the kill of long-finned pilot whales in the western Atlantic mackerel fishery. Waring *et al.* (1989) provide a complete discussion of incidental mortality in this and related fisheries. SC/41/SM19 shows that the spatial distribution of trawl hauls where pilot whales were killed is much smaller than the total range of that fishery. The paper suggests that a sharp increase in the incidental take of pilot whales in 1988 was associated with a contraction of the range of the fishery into the range where pilot whales mortalities have principally occurred in the past.

The sub-committee noted the possibility of reducing the level of incidental mortality by controlling areas allowed for mackerel fishing and **recommended** that more detailed analyses be carried out of both mackerel and pilot whale seasonal distributions to identify suitable areas. The sub-committee also notes with concern that levels of incidental take of pilot whales and other cetaceans were possibly much greater when the mackerel fishery was much larger in the period 1964–74, possibly affecting the status of the cetacean stocks. The sub-committee **recommended** that the data on distribution and season of that fishery be examined to determine if large incidental catches may have occurred.

The sub-committee notes that recent information on the social structure of pilot whales and other odontocetes such as killer whales (Bigg, 1982) suggest that the effects of exploitation may vary with the nature of the fishery. For example, selective fisheries removing young animals from the matriarchal schools may result in increased reproductive rates, while drive fisheries removing whole schools may result in at least temporarily reduced population productiveness (Kasuya and Marsh, 1984). Information on how new schools become established is needed to address this concern and might be obtained from further genetic analysis of schools.

The existence of a past Icelandic drive fishery was confirmed; historical data have been identified. The sub-committee notes that the data on that fishery would be useful and **recommended** that they be obtained and reported.

5.1.8 Status

The level of incidental mortality in the western Atlantic is not well enough known, and the current population estimates have not been available for sufficient examination and do not cover sufficient area, to allow reliable conclusions about status to be drawn. The level of take in the Faroese fishery has been maintained for at least four hundred years, with cyclic fluctuations having a periodicity of about 120 years, and is small relative to the abundance estimates given (SC/41/SM10), but the potential biases in these estimates, and particularly uncertainties concerning net reproductive rates, do not allow status to be assessed with confidence.

5.2 Other populations

5.2.1 Antarctic Ocean

The following papers include information relative to the Antarctic population(s) of pilot whales: SC/41/O 20, SHMi7 and 14, and ProgReps Australia and New Zealand.

SC/41/O 20 provides an estimate of abundance of long-finned pilot whales in the Antarctic south of 60°S, based on sightings during IDCR cruises, of roughly 100,000 (CV 0.7). The estimate was generated using standard line-transect methods developed over the past few years for estimating minke whale abundance. There were relatively few sightings, and the estimate was very sensitive to the manner in which one sighting of about 250 animals close to the trackline was taken into account. The difficulties and uncertainties in this estimate led the sub-committee to question the utility of using these data for determining the distribution and abundance of small cetaceans. It was suggested that better estimates of abundance might be obtained using other analytical procedures, and using the co-distribution of other species.

The importance of using these data, even though they may not be ideal, was emphasised, as there are few other opportunities for studying many of the commercially unimportant species in this region. Further, an understanding of all aspects of the cetacean biomass in the Antarctic may be important in understanding that ecosystem. It was also noted that data from the Japanese sighting vessels operating south of 40°S since 1965 include sightings of many species in addition to the target species. Kasamatsu reported that an analysis of those data is being started.

5.2.2 Other regions

SC/41/SM23 provides a summary of the distribution and abundance of the short–finned pilot whale off the Pacific coast of Canada and concludes that the animals do not appear to be abundant in this area. It was noted that sighting effort is very low, however.

Da Silva reported on the occurrence of *G. melas* off the coast of Brazil. The species cannot be considered common, but strandings and sightings have occurred between 28°50′ and 34°12′S. An apparent stranding of one *G. macrorhynchus* at about 25°S will, if confirmed, constitute the first record of this species in Brazil.

SC/41/ProgRep Japan records sightings and catches of short-finned pilot whales off Japan. Catches totalled 99 whales of the northern form and 493 of the southern form, taken principally by driving, hand-harpoon and small-type whaling. The sub-committee noted take of 28 southern-form whales by small-type whaling methods, an areal expansion of the fishery that probably served to offset the recent decrease in access to large whales. At present the annual take from the southern-form stock represents about 1% of the estimate of abundance in a recent stock assessment (Miyashita, 1986). This estimate, of 53,000 whales, covers an area much larger than that from which the current catch is taken. Because it is possible that inshore and offshore populations are involved in the putative single stock, the sub-committee **recommended** that the stock structure question be addressed before the catches are increased.

Three mass strandings of *G. melas* are reported in SC/41/ProgRep New Zealand and six strandings including one of 13 animals, in SC/41/ProgRep Australia.

Eight long-finned pilot whales, as well as sperm whales and other species, are reported to have been taken incidentally in a new and rapidly growing swordfish gillnet fishery in the Tyrrhenian Sea (SC/41/SM3).

6. NEW INFORMATION ON OTHER STOCKS

6.1 Northern bottlenose whale

The sub-committee reviewed the available information and concluded that re-assessment of the stock would be premature. Gunnlaugsson noted that the estimates of abundance in Icelandic and Faroes waters in SC/40/O 30 Revised are likely biased downward because of lack of adjustment for the long dive times of the species. It was noted that the results of the survey of Norwegian waters reported in SC/41/O 4 are not relevant to bottlenose assessment, because the survey took place in July, when most bottlenose whales have migrated to the south. SC/41/O 22 gives sightings data from Icelandic whalers for the period 1979–88. The frequency of recorded sightings has increased over the period, but the quality of the data needs further investigation. Also, the number of sightings, typically ten to twenty per vessel-season, is insufficient to allow detection of other than very large trends. The paper shows that there is a clear change in the distribution of the animals on the ground west and southwest off Iceland during the season. In the late season the sightings were concentrated at the northwestern boundary of the grounds.

The sub-committee notes that three bottlenose whales were taken in the drive fishery in the Faroes. The sub-committee notes with concern that these catches were taken from a Protected Stock. Bloch reported that she is gathering historical data on the bottlenose whale drive fishery in the Faroese and will report on them at next year's meeting of the sub-committee. The sub-committee agrees that these data will be important in any future assessment and welcomes them.

6.2 Dolphins associated with tuna in the eastern Pacific

Information available to the sub-committee this year included SC/41/SM2, 6 and 29 and reports from scientists from the US National Marine Fisheries Service (NMFS) and the IATTC.

The Scientific Committee last year noted its concern about the continuing high mortality of dolphins when compared to the most recent estimates of absolute abundance and recommended that every effort be made to reduce it and estimate its impact on the stocks, that behavioural and gear research be carried out to lower kill rates, that kills be reported on a stock-by-stock basis, and that the level of biological sampling be increased.

6.2.1 Kill estimates

The incidental kill in 1988 is estimated at 78,927 or 84,881, depending on the the method of calculation (SC/41/SM6). This is lower than the estimated kills in 1986 (by 40%) and 1987 (by 20–25%) but still higher than the estimated kills of the late 1970s and early 1980s (Fig. 1). The sub-committee notes that the estimates have been calculated on a stock-by-stock basis and wishes to thank the IATTC for responding to its recommendation so promptly and fully. Revised estimates for earlier years and details of the methodology used for the 1988 estimate and for the revised estimates are given in Appendix 2. Hall noted that about 3/4 of the reduction in kill over that in 1987 was due to a reduction in fishing effort; he believes that at least part of the remainder of the reduction was due to better performance in dolphin rescue, although changes in dolphin species and stock composition and changes in areal distribution of the fishery may also be responsible. Comparison with the year 1986, which had a level of effort about equal to that in 1988, shows a decrease in kill rates of close to 40%. The sub-committee notes the importance of accurately assessing changes in dolphin-rescue performance and **recommended** that methodology to do this be developed.

The sub-committee notes that the kill of eastern spinner dolphins, perhaps the most depleted stock involved in the fishery (Smith, 1983), has continued at a high level (about 20,000 in both 1987 and 1988) despite the overall reduction in dolphin kill. However, Hall noted that the more recent information available from research-vessel surveys and tuna-vessel observer data does not show any significant change in population abundance over the period covered (1986–88 and 1975–87, respectively). Smith drew attention to the fact that precision was as yet poor from research-vessel data and that there were some unresolved biases in analyses of the tuna-vessel data (Buckland and Anganuzzi, 1988; Edwards and Kleiber, in press) that may relate to interannual changes in spatial distribution in response to environmental conditions, such as seen in 1983 and 1988 (see Item 6.2.4). The sub-committee continues to be concerned about the possible impacts of the kills on the status of the stocks of offshore spotted and common dolphins and **recommended** that the efforts to reduce the kill be continued by all the agencies and nations involved.

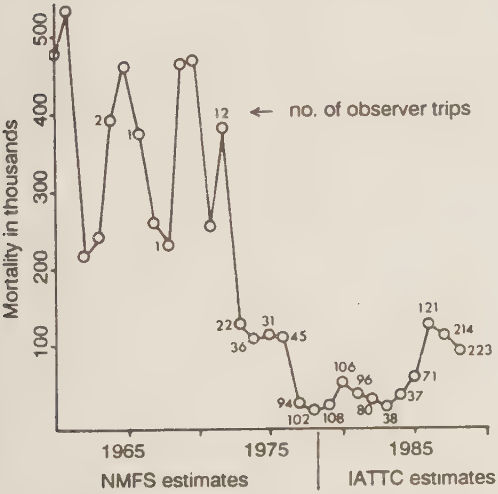

Fig. 1. Estimated incidental mortality of dolphins in the tuna purse-seine fishery in the eastern tropical Pacific, 1960–1988. From IATTC (1989) and SC/41/SM6.

6.2.2 Biological sampling

The Committee last year recommended that biological sampling of the observed kill be increased, to improve estimates of possible trends in growth and reproductive parameters. The proportion of the kill sampled in 1988 was 18%, lower than the 20% of 1987 and the second lowest during the 10-year period 1979–1988 (Table 1). Hohn reported that instructions to the observers changed in mid-1987. In an effort to obtain samples from large-kill sets, which are more representative of population age and sex structures than samples from small-kill sets, the observers now process only carcasses from sets in which 7 or more dolphins (per species) have been killed. In addition, a program offering pay bonuses to observers for collecting samples from more than 30 dolphins when the kill is greater than 30 was started in mid-1988. The results of these initiatives in terms of quality and quantity of the overall sample have not yet been analised, but an analysis will be presented to this sub-committee next year.

Table 1

Biological sampling of dolphins killed incidentally in the tuna purse-seine fishery in the eastern Tropical Pacific, 1979–88. From SC/41/SM2 and earlier reports listed therein.

Year	No. of dolphins biologically sampled	Total observed kill	Propn. of observed kill sampled (%)
1979	2,161	4,900	44.1
1980	1,389	3,125	44.4
1981	1,160	3,297	35.2
1982	1,832	9,262	19.8
1983	750	2,999	25.0
1984	1,166	4,427	26.3
1985	2,293	8,996	25.5
1986	1,277	10,241	12.5
1987	2,874	14,206	20.2
1988	1,881	10,479	18.0

6.2.3 US sightings surveys using research vessels

SC/41/SM31 presented relative abundance indices from the 1988 NMFS survey of ETP dolphin stocks. Under the standard stratified-analysis option, the estimated abundance of the northern offshore stocks of spotted dolphins was 1.92 million, compared with 1.28 million in 1987 and 0.93 million in 1986. The total estimate for common dolphins was 3.11 million in 1988; previous estimates were 0.69 million in 1987 and 1.39 million in 1986. Although the standard errors are large, these estimates indicate very large increases that cannot be explained biologically. By pooling data across geographic strata, fluctuations were appreciably smaller for the northern offshore stock of spotted dolphins, but larger for common dolphins. One of the causes of fluctuations in stock estimates was the detection of several large common dolphin schools in 1988, which increased the estimate of average school size across species from 80–90 animals to 173 animals.

It was noted that estimated size of the eastern stock of spinner dolphin had increased since 1987 and also was higher than earlier estimates. Hall noted that, as discussed above in Item 6.2.1, recent trends in abundance from tuna vessel data also did not indicate a decline; in fact the 1988 estimate was higher than any previous estimates during 1985–87.

Estimates of abundance of SC/41/SM31 for all stocks are affected by the large common dolphin schools recorded in 1988. Concern was expressed that the estimates of one stock are influenced by the data collected on others of different species, including non-target species. This influence might be reduced by, for example, estimating effective search width for all target schools, but estimating other components in the procedure for each species or stock separately. The practice of truncating observations at 2 n.miles from the trackline was queried, as a high proportion of observations is lost. It was noted by the authors that there were problems in fitting the data at greater distances.

Data for Baja neritic and northern common dolphins were pooled in the analyses of SC/41/SM31. There was too little coverage in the Baja area to estimate stocks separately, and they were not distinguished in the field. It was recommended that observers should be trained to differentiate the stocks in future cruises, since this will provide information on the offshore distribution of the Baja neritic stock and on stock boundaries.

It was pointed out that more than half the sightings of (and sets on) southern offshore spotted dolphins by tuna vessels were south of the area searched by research vessels in 1988. This mismatch between the area surveyed for abundance estimation and the area in which the mortality occurred could result in problems in stock assessment. The change in dolphin distribution in 1988 suggests that adjustable stock boundaries might be considered, and that environmental factors are relevant to the analysis.

6.2.4 Relationship between dolphin abundance and oceanographic variables

Reilly reported on the progress of research on the distribution of spotted and common dolphins relative to their environment during 1986/88. There was a moderate El Niño event in 1987, and a strong anti-El Niño in 1988. These years therefore provide a useful contrast. In 1988, the thermocline was particularly shallow in an area extending west along the equator, and research vessel sightings of common dolphins were more numerous there than in the previous two years. Also, in 1988 temperatures in the vicinity of the equator were low, and relatively few spotted dolphins were seen in these areas of lower temperatures. Sightings of spotted dolphins seemed to reflect their preference for a thermocline of intermediate depth. Hall suggested that stratification of sightings could be carried out *a posteriori*, using environmental factors. Reilly noted that they were investigating the possibility of mapping dolphin habitat for each year. The 'habitat' would be identified by relating various environmental variables to dolphin distribution using multivariate techniques.

6.2.5 Efforts to reduce the kill

Hall reported progress in technological research and extension work to reduce kill rates. A new type of small boat propelled by a water-jet engine is being tested on several vessels for use in dolphin rescue in the net; it can cross the corkline and approach the webbing closely without becoming entangled. The results of the trials will be given to the sub-committee next year. He also reported that an international workshop on the dolphin/tuna problem was held in Costa Rica; it was attended by representatives of Colombia, Costa Rica, Ecuador, El Salvador, Spain, France, Guatemala, Japan, Mexico, Nicaragua, Panama, United States, Vanuatu and Venezuela and concentrated on ways to improve performance in dolphin rescue. A second workshop on rescue gear and techniques was organised by Vanuatu for the captains of its fleet of several vessels in Cartagena, Colombia. The Costa Rica meeting also had a session on national legislation, which had been passed recently in attempts to regulate and reduce the dolphin kill.

The sub-committee notes with pleasure the continued effort by the IATTC and the several nations involved toward reduction of the kill.

It is **recommended** that research be continued to be carried out with the objective of improving gear and methods to reduce kill rates.

6.3 Porpoises

The sub-committee agreed to defer consideration of information on phocoenids contained in several documents (SC/41/SM1 and 29; O 5, 12, 22, 25 and 36; ProgReps Denmark, Faroes, FRG, Iceland, Netherlands, Sweden, UK, USA; and SC/40/O 30 Revised) to next year's meeting (see Item 7.3), considering only the information in SC/41/SM25 (because of its relevance to census of all small cetaceans) and ProgRep Japan concerning the great increase in catch of Dall's porpoise.

6.3.1 Line transect survey of harbour porpoise

SC/41/SM25 presents partial results from a survey of harbour porpoise in the Bay of Fundy that was designed to test the applicability of line transect methods to this species. The cruise was designed with comments offered by the sub-committee at last year's meeting on a paper describing a preliminary study (Polacheck and Smith, 1989). The analyses presented suggest a strong vessel avoidance response of animals, although the possibility was noted that this could be due solely to random movement of the animals as seen from a moving platform. The need to conduct a simulation study of the effects of animal movement was noted. The existence of avoidance of research vessels by harbour porpoise in the California Current region was noted, although there the animals appeared to initially move away from the vessel and then in the opposite direction. It was suggested that the data might be analysed to determine if the animals are moving away from the vessel at its current position or away from the vessel's trackline. It was also suggested that the direction of currents might be noted, to determine if the porpoise move with the currents when moving away from the vessel. Further, it was suggested that the experimental survey design of repeating transects in opposite directions might be used to check the movement patterns further. There is also the possibility that harbour porpoise respond to an approaching vessel by increasing their speed of swimming, causing them to rise higher at the surface and become more visible. The effect of this on the detection of avoidance and accuracy of school size estimation was discussed.

6.3.2 The Japanese take of Dall's porpoises

The sub-committee is extremely concerned about the recent very great increase in the catch of Dall's porpoises in Japanese waters, from 13,406 in 1986 (*Rep. int. Whal. Commn* 39:128) to 41,455 last year (SC/41/ProgRep Japan). There is evidence that the porpoise meat is being substituted for whale meat in commerce because of the decrease in access to large whales (Kasuya and Miyazaki, 1989; SC/41/ProgRep Japan). The Committee in previous years has expressed its concern that the (smaller) takes in those years may not have been sustainable (*Rep. int. Whal. Commn* 31:67; 34:57; 35:53).

The increase in catch is mainly in the hand-harpoon fishery and comes from two stocks. With present statistics, the catches cannot be allocated between the two stocks. The two stocks are the Sea of Japan/Okhotsk stock of *dalli*-type porpoises that winters in the Sea of Japan and summers mostly in the Okhotsk Sea and also off the Pacific coast of Hokkaido and the *truei*-type stock that inhabits

Japanese and Soviet Pacific waters (Fig. 2). Estimates of abundance are 47,000+ for the former and 58,000 for the latter, for a total of roughly 105,000+ (Table 2).

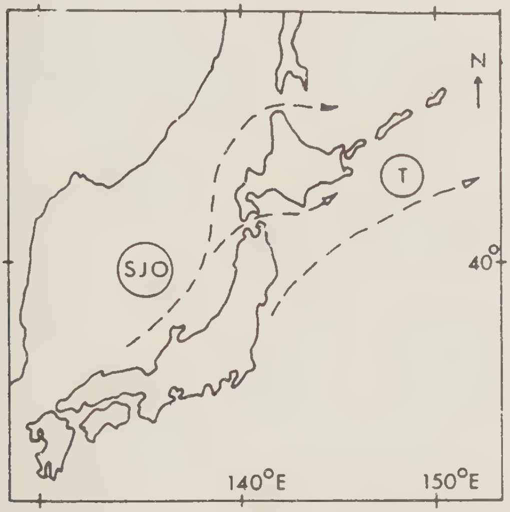

Fig. 2. Seasonal movements of Dall's porpoise and location of the Dall's porpoise fishery in Japanese waters. SJ/0 = Sea of Japan/Okhotsk Sea stock. T = *truei*-type stock. From Kasuya and Miyashita (1989).

Table 2

Estimates of abundance for stocks of Dall's porpoise exploited in the Japanese hand-harpoon fishery. From Miyashita and Kasuya (1988).

Stock and component		Abundance
Sea of Japan/Okhotsk Sea stock		
East Sea of Japan (May-June)		32,000 (CV 0.23)
West Sea of Japan (May-June)		(+)
Pacific (July-August)		15,000 (CV 0.50)
Okhotsk (May-June)		A few
	Total	47,000+
Truei-type stock		
Japanese waters (May)		26,000 (CV 0.25)
USSR waters		32,000
	Total	58,000
	Grand Total	105,000+

Kasuya reported that there may be some over-reporting of catch because of the initiation of a licensing system for 1989 and beyond, in which licenses are only being issued to fishermen who report that they took some Dall's porpoises in 1988. However, incidental take from the *truei*-type stock in squid gillnet fisheries by Taiwanese and Korean vessels in the western North Pacific is not reported and is of unknown size. Some porpoises are struck and lost in the hand-harpoon fishery, but the struck-and-lost rate varies with type of vessel and has not been estimated.

The sub-committee concluded that the take is clearly not sustainable. Depending on the stock composition of the catch, the situation may be even worse for one or other of the two stocks than immediately apparent. The sub-committee believes that it is urgent that the catch be at least reduced to the levels of previous years (which themselves may have been too high) and that assessments of status of the stocks be carried out, to determine safe levels of catch for the two stocks independently. The sub-committee also **recommended** that catch statistics be collected and reported on a stock-by-stock basis. A further **recommendation** is that the Republic of Korea be requested to report by-catches of Dall's porpoises (and other cetaceans) in its squid gillnet fishery to the IWC.

6.3.3 Baird's beaked whale

Kasuya reported that the 50% increase in the Japanese national quota of Baird's beaked whales (from 40 to 60 – SC/41/ProgRep Japan) is a one-year emergency increase for the small-type whaling fleet, to partially replace the former catch of minke whales pending settlement of the question of whether or not there will be a take of minke whales in Japanese small-type whaling in the future.

6.2.4 Other species

New information was received on a number of other species, but time limitations prevented substantive review. The species included *Kogia breviceps* (SC/41/ProgRep Australia, Brazil, New Zealand), *Kogia* sp. (SC/41/ProgRep Japan), unidentified ziphiids (SC/41/SHMi14; ProgRep Japan, Australia), *Ziphius cavirostris* (SC/41/SM3; ProgRep Australia, New Zealand), *Berardius arnuxii* (SC/41/ProgRep Australia), *Hyperoodon planifrons* (SC/41/ProgRep Australia), *Mesoplodon* spp. (SC/41/SM29), *M. bidens* (SC/41/O 36), *M. layardi* (SC/41/ProgRep Australia), *M. grayi* (SC/41/ProgRep Australia), *Pontoporia blainvillei* (SC/41/ProgRep Brazil), *Inia geoffrensis* (SC/41/ProgRep Brazil), *Delphinapterus leucas* (SC/41/SM27, 32; O 4, 12; 36; ProgRep Denmark, UK, USSR), *Monodon monoceros* (SC/41/O 36; ProgRep Denmark), *Orcaella brevirostris* (SC/41/ProgRep Australia), *Cephalorhynchus hectori* (SC/41/ProgRep New Zealand), *Steno bredanensis* (SC/41/ProgRep Brazil), *Sotalia fluviatilis* (SC/41/ProgRep Brazil), *Sousa chinensis* (SC/41/ProgRep Australia), *Grampus griseus* (SC/41/SM3, 29; ProgRep Australia, Japan), *Tursiops truncatus* (SC/41/SM3, 29, 33; O 29; ProgRep Australia, Japan, New Zealand, UK, US), *Delphinus delphis* (SC/41/SM29; O 12; ProgRep Australia, Brazil, New Zealand, Spain, US), *Stenella coeruleoalba* (SC/41/SM3; ProgRep Australia, Faroes, Japan, New Zealand, Spain), *S. longirostris* (SC/41/ProgRep Australia), *S. attenuata* (SC/41/ProgRep Australia, Japan), *S. frontalis* (SC/41/ProgRep Brazil), *Lissodelphis peronii* (SC/41/SHMi14; ProgRep New Zealand), *L. borealis* (SC/41/ProgRep Japan), *Lagenorhynchus obscurus* (SC/41/SM29; ProgRep New Zealand), *L. acutus* (SC/41/O 7, 12, 36; ProgRep Denmark, Faroes), *L. albirostris* (SC/41/SM29; O 25, 27, 36; ProgRep Iceland), *L. cruciger* (SC/41/SHMi14), *Lagenorhynchus* spp. (SC/41/ProgRep Netherlands), *Peponocephala electra* (SC/41/ProgRep Australia), *Pseudorca crassidens* (SC/41/SM16; SHMi14; ProgRep Australia, Japan, New Zealand), *Feresa attenuata* (SC/41/ProgRep Australia) and *Orcinus orca* (SC/41/SM20; O 4, 5, 17, 20, 22, 25, 27, 33, 36; SHMi7, 14; ProgRep Australia, Denmark, Faroes, Iceland, Japan, New Zealand, Norway, Spain, UK, US, USSR; SC/40/O 30 Revised).

7. OTHER BUSINESS

7.1 Takes of small cetaceans in 1988

Reported takes are summarised in Appendix 3. The sub-committee notes that these statistics are incomplete; takes in several IWC member nations are known to occur but have not been reported or have been reported incompletely. It is **recommended** that these nations again be requested to submit complete catch statistics to the IWC. For example, SC/41/SM18 and 19 deal with a by-catch of pilot whales and other cetaceans by foreign-flag vessels in the US EEZ. Some of these vessels are from IWC member nations, but the by-catches do not appear in any national progress report.

The sub-committee notes that data from strandings are useful in determining distribution and movements, both necessary to stock assessment, and therefore **recommended** that member nations not having stranding reporting programmes take steps to establish them.

7.2 Publication of documents

The following documents are recommended for possible publication in a special volume on pilot whales: SC/41/SM4, 5, 7, 8 (in part, combined with 7), 9, 10, 11, 13, 14 (in part, combined with other papers), 15, 17, 18, 19, 21, 22, 23, 26, 28, 30. Other papers developed from documents submitted to the sub-committee will be considered for publication in the volume, as will papers on pilot whales which have not been previously submitted to the sub-committee. The deadline for submission of the papers in revised form to the Scientific Editor is January 1 1990. A list of papers recommended for possible publication in *Rep. int. Whal. Commn* 40 was submitted to the Editorial Board.

7.3 Priority topics for 1990 meeting

The sub-committee proposes to review populations of phocoenids at the next meeting.

7.4 Convention on Migratory Species

Johnson and Ford explained the plans in CMS for conducting a global review of the status of small cetaceans. The review will have the objective of identifying species and populations whose conservation status would benefit from regional agreements among parties and non-parties to the Convention. A small-cetaceans working group is now being established and will provide expert guidance to the Convention's Scientific Council on the review. The review itself may be initially undertaken by a consultant or other expert for further discussion and, if necessary, refinement by the working group and endorsement by the Scientific Council. It was stressed that advice is welcome from the sub-committee or any of its members.

REFERENCES

Andersen, L.W. 1988. Electrophoretic differentiation among local populations of the long-finned pilot whale, *Globicephala melaena*, at the Faroe Islands. *Can. J. Zool.* 66:1884–1992.

Bigg, M. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. int. Whal. Commn* 32:655–70.

Brown, S.G. 1961. Observations of pilot whales (*Globicephala*) in the North Atlantic Ocean. *Norsk Hvalfangst-Tid.* 50(6):225–254.

Buckland, S.T. and Anganuzzi, A.A. 1988. Estimated trends in abundance of dolphins associated with tuna in the eastern tropical Pacific. *Rep. int. Whal. Commn* 38:411–37.

Edwards, E. and Kleiber, P. In press. [The TOPS model]. *Fish. Bull.*

Evans, P.G.H. 1980. Cetaceans in British waters. *Mamm. Rev.* 10:1–52.

Hay, K. 1982. Aerial line-transect estimates of abundance of humpback, fin, and long-finned pilot whales in the Newfoundland-Labrador area. *Rep. int. Whal. Commn* 32:475–88.

IATTC. 1989. Tuna-dolphin Workshop, 14–16 March, 1989, San Jose, Costa Rica. IATTC, La Jolla, Calif., irreg. pag.

Jonsgård, A. 1977. Tables showing the catch of small whales (including minke whales) caught by Norwegians in the period 1938–75, and large whales caught in different North Atlantic waters in the period 1896–1975. *Rep. int. Whal. Commn* 27:413–26.

Kasuya, T. and Marsh, H. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. int. Whal. Commn* (special issue 6):259–310.

Kasuya, T. and Miyashita, T. 1989. [Japanese dolphin fishery and the stock management]. *Collecting and Breeding* 51(4):154–60. [in Japanese]

Martin, A.R., Reynolds, P. and Richardson, M.G. 1987. Aspects of the biology of pilot whales (*Globicephala melaena*) in recent mass strandings on the British coast. *J. Zool., Lond.* 211:11–23.

Mercer, M.S. 1975. Modified Leslie-Delury population models of the long-finned pilot whale (*Globicephala melaena*) and annual production of the short-finned squid (*Illex illece-brosus*) based on their interaction at Newfoundland. *J. Fish Res. Bd Can.* 32:1145–54.

Miyashita, T. 1986. Abundance of some globicephalid cetaceans in the adjacent waters of Japan. Paper SC/38/SM17 presented to the IWC Scientific Committee, June 1986.

Miyashita, T. and Kasuya, T. 1988. Distribution and abundance of Dall's porpoise off Japan. *Sci. Rep. Whales Res. Inst. (Tokyo)* 39:121–50.

Polacheck, T. and Smith, T. 1989. A proposed methodology for field testing line transect theory for shipboard surveys of cetaceans. *Rep. int. Whal. Commn* 39: 341–5.

Sergeant, D.E. 1962. The biology of the pilot or pothead whale (*Globicephala melaena*) in New Foundland waters. *Fish. Res. Bd Can. Bull.* 132:1–83.

Sigurjónsson, J. and Leatherwood, S. (eds). 1988. North Atlantic killer whales. *Rit Fisk.* 11:1–317.

Smith, T.D., Payne, P.M., Heinemann, D.W., Waring, G.T. and Lange, A. 1988. Utility of cetacean and seabird sighting surveys conducted during fishery surveys. *Int. Cons. Expl. Seas* (ICES), C.M.1988/N:L5, 40pp.

Waring, G.T., Parry, B.L., Nicolus, J.R., Gerrior, P. and Payne, P.M. 1989. Incidental take of marine mammals in foreign fishery activities off the northeast USA, 1977–1988. *Fish. Bull. US*: in press.

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Annex Q
Report of the Steering Committee on the Proposed Meeting on Mortality of Cetaceans in Fishing Nets and Traps

W.F. Perrin

The Steering Committee (Perrin, Brownell, Harwood, Kasuya, Arnbom and Braham [*vice* L. Jones]), members of the local organising committee (DeMaster and Barlow) and others interested met to review progress.

BACKGROUND

The Committee last year developed terms of reference for the meeting (*Rep. int. Whal. Commn* 39:153) and recommended that it be funded (*Rep. int. Whal. Commn* 39:63). The Commission approved the meeting in principle but postponed it because of budgetary limitations and a wish to give primary emphasis to immediate needs for the Comprehensive Assessment (*Rep. int. Whal. Commn* 39:27).

TIME AND PLACE OF THE MEETING

The group agreed that at least one year of lead time will be required to ensure the participation of the experts and organisations recommended for inclusion and for preparation of invited papers. Further, it was recognised that the meeting would be best postponed until after the 1990 meeting of the Scientific Committee, to minimise conflict with the Comprehensive Assessment and preparations for it. Mid-January 1991 is proposed. Perrin reported that the invitation extended last year by the Southwest Fisheries Center to hold the meeting in La Jolla, California, still stands.

FUNDING

The budget for the meeting was estimated last year at £30,000. It was agreed and emphasised that commitment of funds by the Commission must be made this year if the meeting is to be held in January 1991 with adequate lead time.

Arnbom announced that WWF-Sweden has agreed to contribute £5,000 towards the costs of the meeting. It was agreed to continue to seek multinational endorsement and support from other organisations in addition to the IWC. Possibilities suggested included UNEP, FAO, IUCN, IOC, CMS, non-governmental organisations and national agencies such as the US Marine Mammal Commission, US National Marine Fisheries Service, Japan Fisheries Agency and Australian National Parks and Wildlife Service. The group noted that the IUCN Species Survival Commission's Cetacean Specialist Group has recommended that the meeting be held and given it high priority in its current action plan (Perrin, 1988).

NEW INFORMATION

The group reviewed substantial new information on incidental kill of cetaceans in gillnets and other fishing gear contained in documents for this meeting and other sources. At least 15 sperm whales and 101 other cetaceans died in a new gillnet fishery for swordfish in Italian waters during less than three years (SC/41/SM3); the total is possibly much larger, because only a fraction of the area of this fishery was covered by the salvage effort. Darling (1988) reported entanglement of a sperm whale in a gillnet near Hawaii. Heyning reported that a dead adult male sperm whale entangled in gillnetting washed ashore in northern California in 1988. Arnbom reported entanglement of a sperm whale in gillnets in the Azores in 1986 and a humpback whale in a gillnet in the Swedish Baltic in 1984. Sixty-one gray whales, four minke whales, two humpback whales, two unidentified balaenopterid whales and two unidentified large whales were documented as entangled in gillnets along the Southern California coast in the 1980s (SC/41/PS14). Again, the coverage is only partial; for example, although the sample size is very small, extrapolation to the entire area of the fisheries involved yields an estimate of 441 rorquals for the period 1980–85. R. Holt reported that the USA Right Whale Recovery Plan (presently in draft form) notes that a large proportion of right whales in the northwest Atlantic show scars thought to be due to fishing gear, including lobster pot lines. Braham reported that 64 humpback whales were entangled in fishing gear off Eastern Canada in 1988; 50 were released alive (*Rep. int. Whal. Commn* 39:189). Over the period 1979–88, 429 were entangled and 81 died. On the US east coast, 20 were entangled between 1975 and 1986 of which 6 died. Off the Pacific coast of Canada and Alaska, 23 were entangled and 1 died during 1984–88. Eight minke whales, four unidentified mysticetes and 3,317 other cetaceans were reported taken incidentally in fishing gear in Japanese waters in 1988 (SC/41/ProgRep Japan). These and other such incidental takes reported by Langelier *et al.* (1988) and in SC/41/SM1, SM23, SM29, ProgReps Australia, Iceland, New Zealand, Sweden and USA, reinforce the conclusion that incidental mortality, especially in gillnets and fish traps, could well be a significant factor for some stocks of whales and should be addressed in an organised and concerted way.

REFERENCES

Darling, J.D. 1988. Working with whales. *Nat. Geogr.* 174(6):886–909.

Langelier, K.M., Stacey, P.J., Baird, R.W. and Marchetti, R. 1988 : 1987 cetacean strandings in British Colombia. Proc. Joint Conf. Amer. Assoc. Zoo Vet. and Amer. Wildl. Vet., November 6–10, 1988, Toronto, Ontario.

Perrin, W.F. (compiler). 1988. Dolphins, Porpoises, and Whales. An Action Plan for the Conservation of Biological Diversity: 1988–1992. IUCN, Gland, Switzerland, 30pp.

Report of the Cetacean Specialist Group

William F. Perrin

This will be a short report. Simon Stuart noted we issued an Action Plan last year, covering the 5-year period 1988-1992. I have a copy here. I also have here a copy of the proceeding volume for a workshop that we organized in China in 1986. This came out in June and is available from IUCN Publication Services.

Our Action Plan concentrates on the small cetaceans, because we believe that the greatest problems are there. Some of the small cetaceans are in imminent danger of extinction, in particular some of the river dolphins.

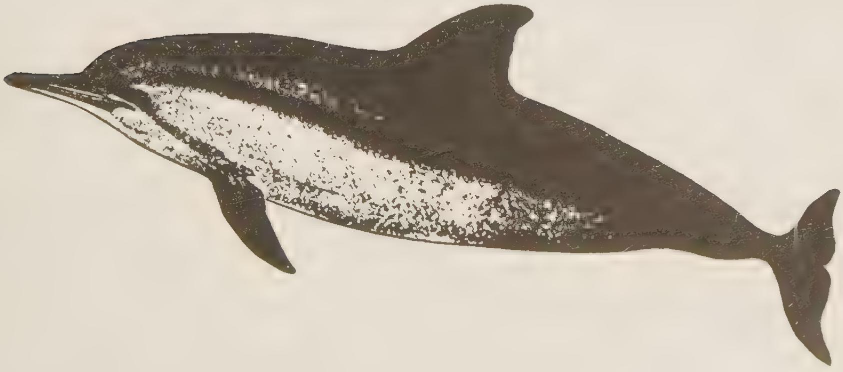
The plan lists 44 specific projects and actions that the Group believes should go forward. We consider 11 to be of the highest priority. Most of these (8) are concerned with river dolphins: the remaining three relate to the incidental kill of vaquitas in the Gulf of California, the illegal use of small cetaceans for crab bait in southern South America, and the need for a workshop on gillnets and cetaceans.

We cannot say that our progress in implementing the plan has been tremendous, but we can report some achievements for several of the recommended actions, and I'll summarize these very briefly.

Project 15. We recommended that the status of the common dolphin in the western Mediterranean be assessed because of a possible great decline in the population there. This was to include research on the stock identity of dolphins in the western Mediterranean and the adjacent North Atlantic. Alex Aguilar of the University of Barcelona has received a grant from the National Science Foundation (NSF) U.S.-Spain Program to begin the work, using tagging and sighting surveys, and the first report will be due in October.

Project 35. One of the high-priority items for the severely endangered baiji, or Chinese river dolphin, is to determine individual movements and population structure. Bernd Wuersig of Texas A & M University has begun this work with funding from WWF, under a joint research agreement with the Academia Sinica and Nanjing Normal University. In addition, the International Whaling Commission (IWC) funded two Chinese students to attend the recent IWC-sponsored workshop on photo-identification methods for cetacean assessment, and they have returned to China and made a good start on cataloguing the individual dolphins in the baiji population (about 300).

Project 36. Also, Professor Zhou Kaija of Nanjing Normal University has just informed me that he has received funding from WWF for



continuing monitoring trends in abundance, for photo-identification, and for grass-roots work in education.

Project 39. We are happy to report that good progress has been made toward saving Hector's dolphin, which is endemic to New Zealand. The New Zealand government has established a sanctuary to protect the species from gillnetting and has started programs to monitor trends in abundance and to obtain better information on kill rates. This has been primarily due to the efforts of Steve Dawson and Elizabeth Slooten of Canterbury University in Christchurch, but the international expressions of concern seem to have helped.

Project 40. Many of the problems that cetaceans face are caused by fisheries, and some of the worst problems are caused by gillnets. We recommended that an international workshop be convened to examine the problem of gillnets and cetaceans. We are very happy to announce that the meeting will take place in September, next year, in La Jolla, California. It will be organized by the Scientific Committee of the IWC and hosted by the Southwest Fisheries Center of the U.S. National Marine Fisheries Service. We now have about 1/2 of the $40,000 that we need for the meeting. The funds have come from WWF-Sweden, the Southwest Fisheries Center, and the U.S. Marine Mammal Commission. Other organizations have indicated interest, including national agencies and UNEP, and we have high hopes. The charges to the workshop will be to identify new and expanding fisheries that kill cetaceans, to design programs to collect adequate statistics on the kills, and to discuss possible ways to reduce the kills through technological research and innovative management. It will be especially important to involve participants from the developing nations that are placing high priority on coastal and offshore fishery development. The amount of money we are able to raise will determine how many of these people we can include. So we do have significant progress on 5 projects.

The 44 projects listed in the action plan will cost in total about $1 million. So far, we've succeeded in raising only a small fraction of that. Ninety percent of the projects remain to be initiated. Many of these relate to situations where species or populations most definitely will disappear in this century unless there is intervention. The most severe crises are in the Indian sub-continent and in China. The most recent news is that the susu has disappeared from the Karnaphuli River above the Kaptai Dam in Bangladesh, apparently because of poaching. This is a very large piece of habitat, now empty of dolphins. In another piece of grim news, it is estimated that construction of the proposed Three Gorges Dam on the Yangtze River will destroy dolphin habitat along 200 km of the river below the dam and reduce the carrying capacity of another 150 km of the river by 41-71%.

We need to move on these projects, and the Cetacean Specialist Group would very much welcome any assistance or advice on how to proceed.

William F. Perrin
Chairman, Cetacean Specialist Group

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Case 2717

Steno attenuatus Gray, 1846 (currently *Stenella attenuata*; Mammalia, Cetacea): proposed conservation of the specific name

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Abstract. The purpose of this application is to conserve the specific name of the pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846), the type species of *Stenella* Gray, 1866. The specific name is threatened by three subjective synonyms, only one of which has been mentioned (as a probable synonym) during this century.

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1. The currently used specific name of the pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846), has a number of subjective synonyms. These include *Delphinus velox* G. Cuvier, 1829, *D. pseudodelphis* Schlegel, 1841, *D. brevimanus* Wagner, 1846, and *Steno capensis* Gray, 1865. It is not known which of the two names *attenuatus* Gray, 1846 or *brevimanus* Wagner, 1846 has priority.

2. The name *Delphinus velox* was proposed for a new species of dolphin by G. Cuvier in 1829. It was used by Fischer (1830, p. 455), F. Cuvier (1836, p. 154), Rapp (1837, p. 30), and was mentioned by Gray (1850, p. 132, where it appeared as a 'species requiring further examination') and Pucheran (1856, pp. 453–456). Trouessart (1898, p. 1035) placed it tentatively as a synonym of *D. malayanus* Lesson in Lesson & Garnot, 1826 (p. 184, pl. 9, fig. 5), considered by Perrin et al. (1987, p. 111) to be a nomen nudum (but more properly a nomen dubium). Ellerman & Morrison-Scott (1951, p. 732) repeated Trouessart's synonymy. Hershkovitz (1966, p. 32) placed *D. velox* as a synonym of *D. dubius* G. Cuvier, 1812 (p. 14; also considered to be a nomen nudum by Perrin et al. (1987, p. 111), but, again, more properly a nomen dubium). Perrin et al. (1987, p. 112) identified the holotype specimen of *D. velox* (a mounted skin in the Muséum National d'Histoire naturelle in Paris, No. 17 of the *Catalogue de la Galerie de Zoologie*) as a pantropical spotted dolphin, *Stenella attenuata*. The specific name *velox* G. Cuvier, 1829 is therefore a senior subjective synonym of *attenuatus* Gray, 1846, but the former has not been applied to spotted dolphins during this century.

3. The name *Delphinus pseudodelphis* was used by Wagner (1846, p. 332) in his revision of Schreber's *Säugethiere*. Wagner ascribed the name to Wiegmann and stated that it was based on the plate (pl. 358) of three views of a skull, which he was now publishing, and that Wiegmann had not provided a description. Volume 7 of the work, in which the name appeared, was begun by Wiegmann, continued by Stannius, and finished by Wagner (Wagner, 1846, p. iv) and was finally published in 1846 (see also Sherborn, 1891, p. 591). Wiegmann's plates, however, were ready several years earlier, and Schlegel (1841, p. 22) referred to '*Delphinus pseudodelphis*, Wiegman [sic] im Schreber, Säugth. Tab. 358'. Schlegel compared the skull with that of other species and considered that it was closest to *D. malayanus*. He ascribed a skull in the collections of

the Leiden museum to the species. Wagner (1846, p. 332) further described the skull and cited Schlegel's paragraph. Schlegel's 1841 work makes the name *pseudodelphis* available and it should therefore be attributed to him, although hitherto authors have ascribed authorship to Wiegmann '1840 or earlier' (Hershkovitz, 1966, p. 32), or Wiegmann in Schreber (1846). Gray (1850, p. 130), True (1889, pp. 67, 69) and Beddard (1900, p. 260) considered it to be a synonym of *attenuatus*, while Trouessart (1898, p. 1035) thought it was a synonym of *malayanus*. Later, True (1894, pp. 36–37) considered *pseudodelphis* to be a nomen nudum. Oliver (1922, p. 583) stated that 'probably it should be united with *S [tenella] malayanus* Lesson (1826) and *S. fraenatus* F. Cuvier (1836)' (actually *D. froenatus* G. Cuvier, 1829, regarded by Perrin et al. (1987, p. 112) as a junior synonym of *Delphinus* (now *Stenella*) *frontalis* G. Cuvier, 1829). Hershkovitz (1966, p. 32) placed the species in the synonymy of *dubius* G. Cuvier, 1812. Perrin et al. (1987, p. 113) identified the skull in the original illustration published by Wagner as that of a pantropical spotted dolphin, the name *pseudodelphis* therefore being a senior subjective synonym of *attenuatus* Gray, 1846. They recommended that as *pseudodelphis* had been discussed only once in this century (by Oliver, 1922, p. 583, in a qualified way, as mentioned above) it should not be resurrected.

4. The name *Delphinus brevimanus* was used by Wagner in 1846 in the caption to a colored plate of a dolphin (pl. 361, fig. 2) and in the index of plates (p. 427). A plate of a dolphin (pl. 21, fig. 2), together with views of a skull (pl. 23, figs. 7 and 8), both labeled 'Dauphin à Petites Pectorales', appeared in the zoological part of the *Atlas* of the *Voyage au Pôle Sud, Astrolabe et la Zélée* (Hombron & Jacquinot, 1842–1853). Subsequently, the text of the zoological part was published (1853) and the species was referred to (p. 38) as 'Dauphin à Petites Pectorales Hombron & Jacquinot, pl. 21, fig. 2; *Delphinus brevimanus* Wagner, Schreb. Säug., pl. 361, fig. 2'. The skull figured by Hombron & Jacquinot is No. 1882–113 in the Muséum National d'Histoire naturelle in Paris. Gray based his species *Delphinus? microbachium* (1850, p. 119) on this skull and referred to Hombron & Jacquinot's plates; he subsequently included the species as *Steno? brevimanus* in his 1866 *Catalogue of Seals and Whales* (p. 236; reference 1866a) but not in his 1868 *Synopsis*. *D. brevimanus* was also included by Gervais (1877, p. 605). True (1889, p. 67) placed it in the synonymy of *malayanus*, as also did Trouessart (1898, p. 1035). It was not recognized by Beddard (1900). Hershkovitz (1966, p. 33) thought it a synonym of *dubius*, while Perrin et al. (1987, p. 114) placed it in the synonymy of *attenuatus*. The name *brevimanus* has not been used as a senior synonym during this century.

5. The specific name *attenuatus* was first used by Gray in 1843 (p. 105) in combination with *Delphinus* but without description or figure and it was, therefore, a nomen nudum. Gray subsequently (1846, p. 44, pl. 28), based *attenuatus* on a juvenile skull of unknown provenance, No. 347b, in the British Museum (Natural History) and included it in his new genus *Steno* (1846, p. 43). The specific name *attenuatus* has been widely used for the pantropical spotted dolphin for many years. After its application by True to spotted dolphins from the Atlantic (1889, p. 165), the Indian Ocean (1894) and the Pacific (1903, p. 43), it was used by Fraser (1950), Hohn & Hammond (1985), Honacki et al. (1982, p. 296), the International Whaling Commission (1977–1988), Jones et al. (1986, p. 17), Leatherwood et al. (1983, p. 230), Miyazaki et al. (1974), Nishiwaki (1967, pp. 5, 36), Nishiwaki et al. (1965), Nowak & Paradiso (1983, p. 877 and others), Perrin (1975a, pp. 125, 128; 1975b, pp. 1061–1063; 1984, pp. 137, 138;

1988), Perrin et al. (1976; 1979; 1985, pp. 4, 21, 23), Rice (1977, pp. 8, 13) and others. Substitution of any of the synonyms *velox*, *pseudodelphis* or *brevimanus* for *attenuatus* would upset long-standing nomenclatural stability for this well-known pantropical species and cause considerable confusion in the zoological literature, in legal and institutional documentation, and in the legislative language relating to conservation and management of the species.

6. The name *Delphinus capensis* Gray, 1828 (p. 2) was based on a dolphin skin from the Cape of Good Hope in the British Museum (Natural History). Subsequently, Gray (1865, p. 522) proposed the name *Steno capensis* for a dolphin skull in the South African Museum, Cape Town which was later presented to the British Museum (Natural History). The two specific names *capensis* were proposed for species included in different genera (*Delphinus* Linnaeus, 1758 and *Steno* Gray, 1846) and are still regarded as distinct today. *Delphinus capensis* Gray, 1828 is presently treated as a junior synonym of *Delphinus delphis* Linnaeus, 1758 (Hershkovitz, 1966, p. 43). True (1889, p. 62), Hershkovitz (1966, p. 33) and Perrin (1987, p. 150) listed *S. capensis* Gray, 1865 as a junior subjective synonym of *attenuatus*. There is thus no doubt that *Delphinus capensis* Gray, 1828 is not a senior subjective synonym or secondary homonym of *Steno capensis* Gray, 1865.

7. The name *Prodelphinus* was proposed by Gervais (in Van Beneden & Gervais, 1880, p. 604) for a genus distinct from *Delphinus* by the absence of deep palatine lateral grooves. True (1889, pp. 61–62) included 23 species in the genus, including *attenuatus*. Subsequently, Oliver (1922, p. 582) adopted *Stenella*, a name proposed by Gray (1866b, p. 213) for the single species *Steno attenuatus*, as a name senior to *Prodelphinus*. *Stenella* was poorly defined and was not listed by Simpson (1945) but under Article 12(b)(5) of the Code is an available name. Following its use by Iredale & Troughton (1934, p. 65), Fraser (1950), Fraser & Purves (1960), and others it has been universally accepted (see, for example, Corbet & Hill (1986, p. 123)). *Steno* Gray, 1846 is now confined to a single species, *Steno bredanensis* Lesson, 1828 (a replacement name for *Delphinus rostratus* Desmarest, 1817 which was preoccupied), the rough-toothed dolphin with a wide distribution in tropical and warm temperate seas (Hershkovitz, 1966, p. 15).

8. The International Commission on Zoological Nomenclature is accordingly asked:

(1) to use its plenary powers to suppress the following specific names for the purposes of the Principle of Priority but not for those of the Principle of Homonymy:
    (a) *velox* G. Cuvier, 1829, as published in the binomen *Delphinus velox*;
    (b) *pseudodelphis* Schlegel, 1841, as published in the binomen *Delphinus pseudodelphis*;
    (c) *brevimanus* Wagner, 1846, as published in the binomen *Delphinus brevimanus*;

(2) to place on the Official List of Generic Names in Zoology the name *Stenella* Gray, 1866 (gender: feminine), type species by monotypy *Steno attenuatus* Gray, 1846;

(3) to place on the Official List of Specific Names in Zoology the name *attenuatus* Gray, 1846, as published in the binomen *Steno attenuatus* (specific name of the type species of *Stenella* Gray, 1866);

(4) to place on the Official Index of Rejected and Invalid Specific Names in Zoology the following names:
  (a) *velox* G. Cuvier, 1829, as published in the binomen *Delphinus velox* and as suppressed in (1)(a) above;
  (b) *pseudodelphis* Schlegel, 1841, as published in the binomen *Delphinus pseudodelphis* and as suppressed in (1)(b) above;
  (c) *brevimanus* Wagner, 1846, as published in the binomen *Delphinus brevimanus* and as suppressed in (1)(c) above.

References

Beddard, F. E. 1900. *A Book of Whales*. 320 pp. John Murray, London.

Corbet, G. B. & Hill, J. E. 1986. *A World List of Mammalian Species*. Ed. 2, 254 pp. Facts on File Publications & British Museum (Natural History), New York & London.

Cuvier, F. 1836. *De l'histoire naturelle des Cétacés*. iv, 416 pp.; atlas 8 pp., 22 pls. Roret, Paris.

Cuvier, G. 1812. Rapport fait à la classe de Sciences mathématiques et physiques, sur divers Cétacés pris sur les côtes de France, principalement sur ceux qui sont échoués près de Paimpol, le 7 janvier 1812. *Annales du Muséum National d'Histoire Naturelle*, **19**: 1–16.

Cuvier, G. 1829. *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à d'anatomie comparée*. 2nd Ed., vol. 1. 584 pp. Deterville, Paris.

Ellerman, J. R. & Morrison-Scott, T. C. S. 1951. *Checklist of Palaearctic and Indian Mammals 1758–1946*. 810 pp. British Museum (Natural History), London.

Fischer, J. B. 1830. *Addenda, Emendanda et Index ad Synopsis Mammalium*. Pp. 329–456, 657–752. Cotta, Stuttgart.

Fraser, F. C. 1950. Description of a dolphin *Stenella frontalis* (Cuvier) from the coast of French Equatorial Africa. Pp. 61–84, pls. 6–9 *in Atlantide Report* No. 1. *Scientific Results of the Danish Expedition to the Coast of tropical West Africa 1945–1946*. Danish Science Press, Copenhagen.

Fraser, F. C. & Purves, P. E. 1960. Hearing in Cetaceans. Evolution of the accessory air sacs and the structure and function of the outer and middle ear in Recent cetaceans. *Bulletin of the British Museum (Natural History), Zoology*, **7** (1): 1–140, 53 pls.

Gervais, H. 1880. Pp. 601–634 *in* Van Beneden, [P.] J. & Gervais, P. [1868–1880]. *Ostéographie des Cétacés vivants et fossiles*. 634 pp., 64 pls. (published and distributed 1868–1869). Bertrand, Paris.

Gray, J. E. 1828. *Spicilegia Zoologica; or original figures and short systematic descriptions of new unfigured animals*. Part 1, 8 pp., 6 pls. Treuttel, Wurtz & Co., & W. Wood, London.

Gray, J. E. 1843. *List of the Mammalia in the Museum*. British Museum, London. xxviii, 216 pp.

Gray, J. E. 1846. On the Cetaceous animals. Pp. 13–53, 37 pls. *in* Richardson, J. & Gray, J. E. (Eds.). *The Zoology of the Voyage of H.M.S. 'Erebus' and 'Terror' during the years 1839 to 1843*, vol. 1. Mammalia, Birds. Janson, London.

Gray, J. E. 1850. *Catalogue of the specimens of Mammalia in the collections of the British Museum*. Part 1, Cetacea. xii, 153 pp., 8 pls. British Museum, London.

Gray, J. E. 1865. Notices of a new genus of delphinoid whales from the Cape of Good Hope, and of other cetaceans from the same seas. *Proceedings of the Zoological Society of London*, **1865**: 522–529.

Gray, J. E. 1866a. *Catalogue of Seals and Whales in the British Museum*. 402 pp. British Museum, London.

Gray, J. E. 1866b. Notes on the skulls of dolphins, or bottlenose whales, in the British Museum. *Proceedings of the Zoological Society of London*, **1866**: 211–218.

Gray, J. E. 1868. *Synopsis of the species of whales and dolphins in the collection of the British Museum*. 10 pp., 37 pls. Quaritch, London.

Hershkovitz, P. 1966. Catalog of living whales. *United States National Museum, Bulletin*, **246**: 1–259.

Hohn, A. A. & Hammond, P. S. 1985. Early postnatal growth of the spotted dolphin. *Stenella attenuata*. in the offshore eastern tropical Pacific. *Fishery Bulletin*, **83** (4): 553–566.

Hombron, [J. B.] & Jacquinot, H. 1842–1853. *Atlas* of the *Voyage au Pôle Sud et dans l'océanie sur les corvettes 'l'Atrolabe' et 'la Zélée' pendant les années 1837–1838–1839–1840 sous le commandement de M. J. Dumont-D'Urville*. Zoologie, part 1 (Vertebrata). 70 pls. Gide & Baudry, Paris.

Honacki, J. H., Kinman, K. E. & Koeppl, J. W. 1982. *Mammal Species of the World. A taxonomic and geographic reference*. 694 pp. Allen Press & the Association of Systematics Collections. Lawrence, Kansas.

International Whaling Commission. 1977–1988. Reports of the International Whaling Commission.

Iredale, T. & Troughton, E. Le G. 1934. A check-list of the mammals recorded from Australia. *The Australian Museum, Sydney*, Memoir 6, xi, 122 pp.

Jacquinot, H. & Pucheran, J. 1853. *In* Hombron, [J.B.] & Jacquinot, H. *Voyage au Pôle Sud et dans l'océanie sur les corvettes 'l'Astrolabe' et 'la Zélée'*, vol. 3 (Zoologie). Mammifères et Oiseaux. 107 pp. Gide & Baudry, Paris.

Jones, J. K., Jr., Carter, D. C., Genoways, R. H., Hoffman, R. S., Rice, D. W. & Jones, C. 1986. Revised checklist of North American mammals north of Mexico, 1896. *Occasional Papers. The Museum, Texas Tech University*, No. 107. 22 pp.

Leatherwood, S. & Reeves, R. R. 1982. *The Sierra Club Handbook of Whales & Dolphins*. 302 pp. Sierra Club Books, San Francisco.

Miyazaki, N., Kasuya, T. & Nishiwaki, M. 1974. Distribution and migration of two species of *Stenella* in the Pacific coast of Japan. *Scientific Report of the Whales Research Institute, Tokyo*, **26**: 227–243.

Nishiwaki, M. 1967. Distribution and migration of marine mammals in the North Pacific area. *Bulletin of the Ocean Research Institute, University of Tokyo*, **1**: 1–64.

Nishiwaki, M., Nakajima, M. & Kamiya, T. 1965. A rare species of dolphin (*Stenella attenuata*) from Arari, Japan. *Scientific Report of the Whales Research Institute, Tokyo*, **19**: 53–64.

Nowak, R. M. & Paradiso, J. L. 1983. *Walker's Mammals of the World*. 4th Ed., vol. 2. 1362, xxv pp. John Hopkins University Press, Baltimore & London.

Oliver, W. R. B. 1922. A review of the Cetacea of the New Zealand seas. *Proceedings of the Zoological Society of London*, **1922** (3): 557–585.

Perrin, W. F. 1975a. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography. Technical Series*, **21**: vi, 1–206.

Perrin, W. F. 1975b. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. *Journal of the Fisheries Board of Canada*, **32** (7): 1059–1067.

Perrin, W. F. 1984. Patterns of geographical variation in small cetaceans. *Acta Zoologica Fennica*, **172**: 137–140.

Perrin, W. F. 1988. *Dolphins, porpoises and whales. An action plan for the conservation of biological diversity: 1988–1992*. 29 pp. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.

Perrin, W. F., Coe, J. M. & Zweifel, J. R. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fishery Bulletin*, **74** (2): 229–269.

Perrin, W. F., Mitchell, E. D., Mead, J. G., Caldwell, D. K., Caldwell, M. C., van Bree, P. J. H. & Dawbin, W. H. 1987. Revision of the spotted dolphins, *Stenella* spp. *Marine Mammal Science*, **3**(2): 99–170.

Perrin, W. F., Scott, M. D., Walker, G. J. & Cass, V. L. 1985. Review of Geographical Stocks of Tropical Dolphins (*Stenella* spp. and *Delphinus delphis*) in the Eastern Pacific. *National Oceanic and Atmospheric Administration. Report of the National Marine Fisheries Service (U.S. Department of Commerce, Seattle)*, No. 28. 28 pp.

Perrin, W. F., Sloan, P. A. & Henderson, J. R. 1979. Taxonomic status of the 'southwestern stocks of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata*'. *Report of the International Whaling Commission*, No. 29, pp. 175–184.

Pucheran, J. 1856. Notices mammalogiques. *Revue et Magasin de Zoologie Pure et Appliqué*, (2) **8**: 449–460.

Rapp, W. 1837. *Die Cetaceen zoologisch-anatomisch dargestellt*. 182 pp., 8 pls. Cotta, Stuttgart.

Rice, D. W. 1977. A list of the marine mammals of the world (Third edition). *National Oceanic and Atmospheric Administration. Technical Report. Report of the National Marine Fisheries Service (U.S. Department of Commerce, Seattle). Special Scientific Report-Fisheries*, No. 711. 15 pp.

Schlegel, H. 1841. *Abhandlungen aus dem Gebiete der Zoologie und vergleichenden Anatomie*, vol. 1 (Beiträge zur Characteristik der Cetaceen). 44 pp., 6 pls. Arnz, Leiden.

Sherborn, C. D. 1891. On the dates of the Parts, Plates and Text of Schreber's 'Säugethiere'. *Proceedings of the Zoological Society of London*, **1891** (4): 587–592.

Simpson, G. G. 1945. The Principles of Classification and a classification of Mammals. *Bulletin of the American Museum of Natural History*, **85**: iv, 1–350.

Trouessart, E. L. 1898. *Catalogus mammalium tam viventium quam fossilium*. Vol. 2, part 5 (Sirenia, Cetacea, Edentata, Marsupialia, Allotheria, Monotremata), part 2, pp. v, 999–1469. Friedländer & Son, Berlin.

True, F. W. 1889. Contributions to the natural history of the cetaceans, a review of the family Delphinidae. *United States National Museum Bulletin*, **36**: 1–191, 47 pls.

True, F. W. 1894. Notes on some skeletons and skulls of porpoises of the genus *Prodelphinus* collected by Dr. W.L. Abbott in the Indian Ocean. *Proceedings of the United States National Museum*, **17**: 33–37.

True, F. W. 1903. *Notes on a porpoise of the genus* Prodelphinus *from the Hawaiian Islands*. U.S. Commission of Fish and Fisheries, Government Printing Office, Washington, pp. 41–45, pls. 1 and 2. (Reprinted in 1906, *Bulletin of the United States Fish Commission*, **23** (for 1903)(3): 809–815).

Wagner, J. A. 1846. *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen von D. Johann Christian Daniel von Schreber*, vol. 7 (Ruderfüsser und Fischzitzthiere), vii, 427 pp. Erlangen, Leipzig.

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SUBSPECIES OF *STENELLA LONGIROSTRIS* (MAMMALIA: CETACEA: DELPHINIDAE)

William F. Perrin

Abstract. — Three subspecies of *Stenella longirostris* are named, described and compared: *S. l. longirostris* from the world's tropical oceans, *S. l. orientalis* from tropical oceanic and coastal waters of the eastern Pacific, and *S. l. centroamericana* from Pacific coastal waters of Central America.

In a review of variation in *Stenella* spp. in eastern Pacific and Hawaiian waters (Perrin 1975a) I provisionally delineated four forms of the spinner dolphin:

1. "Costa Rican Spinner Porpoise, *Stenella longirostris* subsp. A (unnamed?),"
2. "Eastern Pacific Spinner Porpoise, *Stenella longirostris* subsp. B (unnamed?),"
3. "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed?)," and
4. "Hawaiian Spinner Porpoise, *Stenella longirostris* subsp. D (unnamed?)."

I did not assign trinomial names to the forms because of a lack of data for spinner dolphins in other parts of the world and uncertainty about the affinities of the holotype specimen of the species. (The holotype is a skull from an unknown locality.) Sufficient data have now accumulated to allow formal description and naming of three subspecies. Two of the subspecies correspond to Nos. 1 and 2 above, and the third includes No. 4. No. 3, the "whitebelly spinner," has proved to be a highly variable hybrid/intergrade between Nos. 2 and 4.

Skull measurements summarized below were taken as described in Perrin (1975a).

Museum acronyms. — ANSP, Philadelphia Academy of Natural Sciences, Pittsburgh, Pennsylvania; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; DKC, personal collection of D. K. Caldwell, Marineland of Florida, St. Augustine; EDM, collection of Edward D. Mitchell; LACM, Los Angeles County Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology, Baton Rouge; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MMBL, National Marine Mammal Laboratory, Seattle, Washington; MNHN, Museum National d'Histoire Naturelle, Paris; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; NSM, National Science Museum, Tokyo; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SDMNH, San Diego Museum of Natural History, San Diego, California; SWFC, Marine Mammal Synoptic Collection, Southwest Fisheries Center, La Jolla, California; TCWC, Texas Cooperative Wildlife Collection, Texas A&M University, College Station; UCMP, Museum of Paleontology, University of California, Berkeley; UF, Florida State Museum, University of Florida, Gainesville; USNM, National Museum of Natural History, Washington, D.C.; ZMA, Zoologisch Museum, University of Amsterdam.

Stenella longirostris longirostris (Gray, 1828)

Holotype. — RMNH 8676, skull only, unknown locality.

Referred specimens. — Hawaiian Islands: CAS 10529, 16455, 16456, 16457, 16458; LACM 27093, 27095, 54049, 54050, 54056, 54057, 54060, 72296; SWFC WFP605, WFP606, WFP623, WFP669, WFP670, WFP671; MCZ 51700; MMBL 1194; NSM 24615, 24815; USNM 339649, 504140, 504470. Christmas Island (Central Pacific): ANSP 19194, 19195. Washington Island: USNM 504251. Rangiroa (Tuamoto Islands): USNM 504252. Hiva Oa (Marquesa Islands): USNM 504253. Enewetok (Marshall Islands): USNM 395404. Western Pacific between 1 and 9°S, 147 and 160°E: NSM M24928, M24929, M24930, M24931, M24933, M24934, M25373. Western Pacific between 3 and 5°N, 142 and 150°E: NSM M25376, M24932. Japan: NSM M05100, M24800. Sri Lanka: BMNH 1891.10.13.2, 1948.4.20.1, 1949.10.27.1 and 2. Maldive Islands: BMNH 1959.7.9.1, 1959.7.9.3, 1959.7.9.4, 1959.7.9.5 and 1959.7.9.6. Ivory Coast: USNM 470557. Liberia: RMNH 21.720. Senegal: ZMA 12.263, 13.146, 13.147, IFAN2; EDM 784. North Carolina: USNM 291352, 504525. South Carolina: USNM 500859. Florida: DKC R-4-SLS; UF 7861, 18719; LSUMZ 17017; Texas: TCWC 28286, 29035; USNM 504224, 504233, 504433–504456. St. Vincent (Lesser Antilles): UF 18720–18724. Venezuela: ZMA 15.138.

Diagnosis.—A subspecies of *Stenella longirostris* characterized by distinct tripartite color pattern (Fig. 1), erect (in adult male) to falcate dorsal fin, relatively small postanal hump, relatively large adult size (to about 215 cm; average about 180–190 cm) and relatively long (394–464 mm) and broad (zygomatic width 150–170 mm) adult skull.

Distribution.—Tropical and subtropical waters of the world. Replaced in the eastern Pacific by *S. longirostris orientalis* and *S. longirostris centroamericana* (described below) and possibly in Southeast Asia/northern Australasia by an undescribed dwarf subspecies (Perrin et al. 1989) with lower average tooth and vertebral counts and in the northwestern Indian Ocean/Red Sea by another locally adapted form (Robineau & Rose 1983). Most common near coasts and islands (Gilpatrick et al. 1987).

Description of holotype.—Measurements (in mm) of the holotype skull: condylobasal length 426, length of rostrum 277, width of rostrum at base 76, width of rostrum at ½ length 48, width of rostrum at ¾ length 36, greatest preorbital width 142, greatest postorbital width 159, zygomatic width 156, parietal width 125, length of left temporal fossa 50, height of left temporal fossa 43, length of left upper toothrow 241, length of left ramus 368, height of left ramus 57. Teeth: upper left 54, upper right 53, lower left 52, lower right 54. External size, shape and coloration unknown.

Variation.—The color pattern is stable except in a broad zone of hybridization/intergradation with *S. longirostris orientalis* in the offshore eastern tropical Pacific (range of the "whitebelly spinner"—Perrin et al. 1985), where coloration and shape may be intermediate between those of the two forms (Fig. 1; Perrin 1972, Perrin, Sloan & Henderson 1979). In these specimens, the cape may be less distinct and the ventral margin of the dorsal overlay (terminology of Perrin 1972) stepped, ragged or grading into ventral spots.

Adult size may vary geographically (Perrin et al. 1989). The largest individual known was from Hawaii (CAS 16456, 213 cm). An adult male hybrid/intergrade from the eastern Pacific (SWFC BGB008) was 235 cm long, but this may have been a case of endocrinally induced gigantism; the next largest in the sample of 262 specimens from the population (including several from the same school) was over 30 cm shorter (Perrin & Gilpatrick 1990). The largest body of external measurements from a single region is from the tropical Atlantic (Perrin et al. 1981): 17 adult females ranged from 177 to 204 cm (average 188.9 cm) and 17 males from 173 to 208 cm (average 192.5 cm); four physically mature males were 192–208

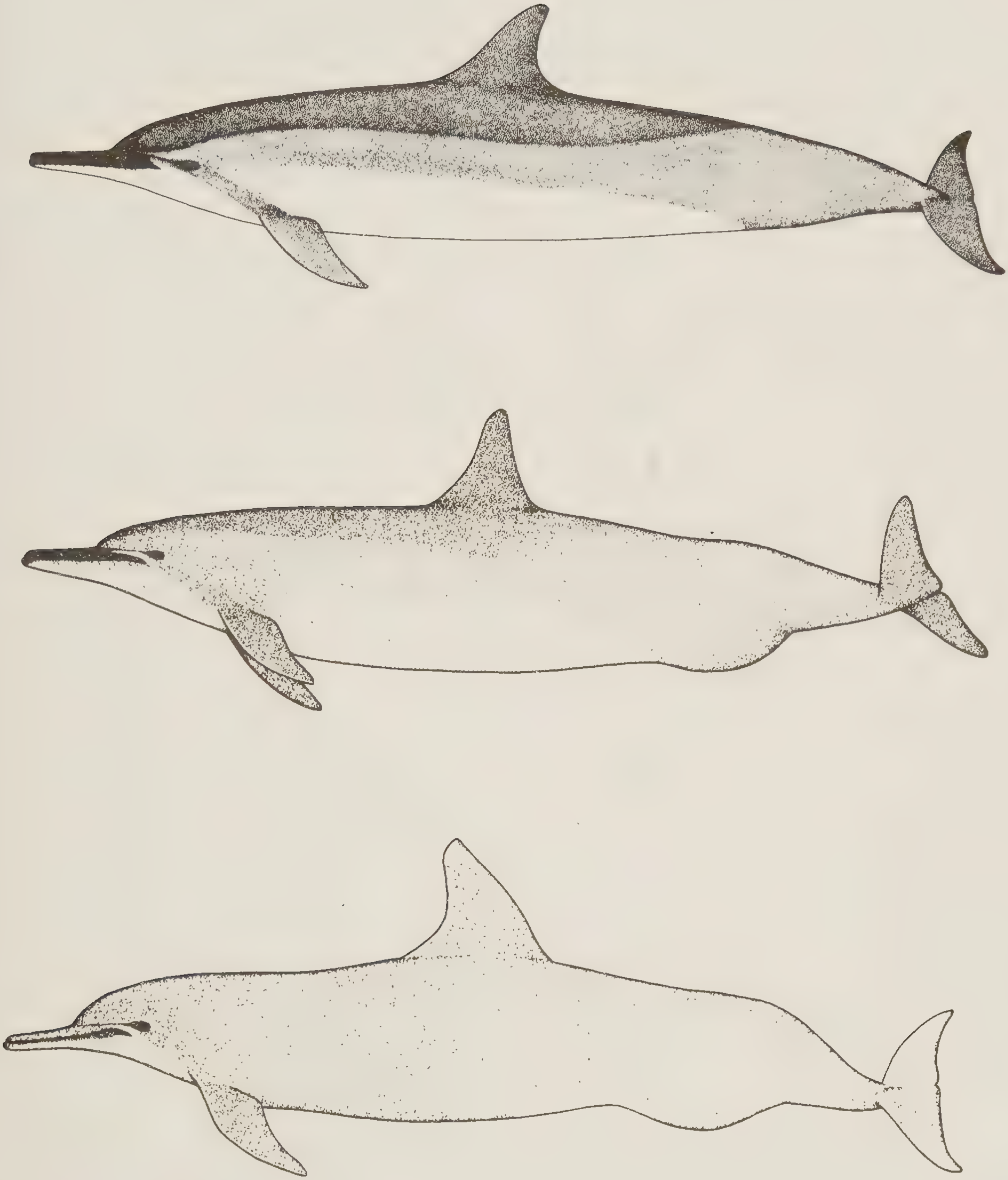

Fig. 1. Typical appearance of adult males of *Stenella longirostris longirostris* (top), *S. l. orientalis* (bottom) and a hybrid/intergrade (center). *S. l. centroamericana* is not illustrated, because the color pattern is not well known.

cm long and two females 196 and 201 cm long.

Skull size may also vary geographically (Table 1), but larger series from more localities will be necessary to demonstrate this adequately. The same is true of tooth counts (Table 1). Skulls from the hybrid/intergradation zone discussed above may be inter-

Table 1.—Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected skull measurements and tooth counts for geographical series of cranially adult specimens of *Stenella longirostris longirostris* (from Perrin et al. 1989). Specimens of dwarf form from Southeast Asia excluded.

	Indian Ocean	Western Pacific	Central Pacific	Atlantic
Condylobasal length	409.2	420.1	436.9	427.0 ± 13.10
	(7) 394–430	(7) 411–431	(24) 417–464	(41) 395–458
Length of rostrum	264.9	272.1	282.6	276.8 ± 11.00
	(7) 250–281	(7) 262–281	(24) 263–304	(41) 251–304
Width of rostrum:				
At base	74.0	78.3	79.3	76.6 ± 3.41
	(7) 71–76	(7) 73–84	(24) 74–86	(42) 68–83
At ½ length	43.3	47.9	47.0	44.4 ± 2.30
	(7) 42–45	(7) 44–54	(24) 42–56	(41) 41–50
At ¾ length	31.0	31.4	32.3	31.9 ± 2.63
	(7) 28–34	(5) 26–36	(24) 27–37	(39) 25–39
Width of PMXs at ½ length	19.4	21.0	21.1	21.0 ± 2.32
	(7) 18–20	(6) 19–23	(24) 17–23	(37) 17–32
Preorbital width	141.6	144.6	150.8	145.6 ± 3.86
	(7) 135–146	(5) 140–150	(24) 140–158	(42) 137–153
Postorbital width	155.4	160.8	165.2	161.1 ± 4.03
	(7) 153–160	(6) 155–169	(25) 158–172	(41) 152–169
Zygomatic width	154.0	156.2	163.5	159.2 ± 3.92
	(7) 151–160	(5) 152–161	(25) 154–171	(40) 150–167
Parietal width	128.7	127.6	131.4	130.5 ± 4.25
	(7) 122–133	(5) 125–131	(25) 122–140	(41) 121–140
Length of temporal fossa	50.0	47.4	53.3	48.1 ± 3.30
	(7) 46–58	(5) 44–51	(25) 45–61	(42) 42–56
Height of temporal fossa	41.4	41.0	42.9	38.3 ± 3.52
	(7) 39–45	(5) 36–44	(25) 37–50	(42) 30–49
Length of upper toothrow	232.3	237.2	245.6	243.5 ± 10.30
	(7) 224–242	(6) 219–246	(24) 224–263	(41) 221–265
Length of ramus	352.0	366.3	372.4	368.4 ± 11.68
	(7) 366–370	(7) 360–371	(23) 352–399	(40) 343–399
Height of ramus	55.9	55.8	58.4	56.4 ± 2.28
	(7) 55–57	(6) 55–57	(23) 53–64	(41) 51–61
Upper teeth (per row)	52.9	53.3	55.0	55.4 ± 3.01
	(15) 49–59	(12) 48–61	(29) 50–62	(41) 48–64
Lower teeth (per row)	50.6	51.4	52.5	53.9 ± 3.32
	(8) 42–49	(15) 45–58	(29) 48–57	(43) 47–62

mediate in size and form between those in this subspecies and in *S. l. orientalis* (Perrin 1975a, Perrin, Sloan & Henderson 1979).

Remarks.—This subspecies includes the "Hawaiian Spinner Porpoise, *Stenella longirostris* subsp. D (unnamed?)" (Perrin 1975a). Hybrids/intergrades with *S. l. orientalis* (described below) correspond to the "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed)" (Perrin 1975a).

Genetic as well as morphological evidence support the hypothesis that the highly variable "northern whitebelly spinner" and "southern whitebelly spinner" (Perrin, Sloan & Henderson 1979, Perrin et al. 1985) represent a zone of hybridization or intergradation between the two distinct forms to the west and the east; "whitebelly spinners" possessed no unique mitochondrial DNA haplotypes when compared with animals to the east (Dizon & Perrin 1987).

Hewitt (1988) noted that the width of many hybrid zones is about one hundred times the estimate of dispersal for the individual organisms. The zone of hybridization/intergradation for *S. l. longirostris* and *S. l. orientalis* (described below) is about 2000 km wide (Perrin et al. 1985). The former tends to inhabit coastal waters and waters around islands (Gilpatrick et al. 1987, Perrin et al. 1983), but tagged oceanic spinner dolphins in the eastern Pacific have moved at least 400 km (Perrin, Evans & Holts 1979). However, as pointed out by Hewitt, gene dispersal rate is likely to vary greatly with population density, structure and patchiness, and more information is needed on these before the significance of the relatively great dispersal distance of individuals relative to the width of the hybridization/intergradation zone can be weighed.

The holotype specimens of two junior synonyms of *S. longirostris* are probably of this form; both are relatively long and broad skulls from unknown localities. These are the holotypes of *Delphinus alope* Gray, 1846 (BMNH 847a; condylobasal length 412 mm, zygomatic width 166 mm) and *D. stenorhynchus* Gray, 1866 (BMNH 1471a; condylobasal length ca. 447 mm, zygomatic width ca. 167 mm). A third holotype specimen, that of *D. microps,* also from an unknown locality (BMNH 349a), is at the lower end of the known range of adult skull length (394 mm) and below (at 147 mm) the range of skull width (150 mm) for this subspecies, suggesting that it belongs to a different form.

It seems likely that the very broadly distributed populations of this form will eventually prove to include several additional locally adapted races sufficiently distinct to merit recognition as subspecies. This seems to almost certainly be the case in Southeast Asia (Perrin et al. 1989) and is possibly the case in the northwestern Indian Ocean (Robineau & Rose 1983). The problem is simply one of material; cetacean specimens are very costly and difficult to collect, prepare and store. In the case of *S. longirostris* the species is known from several very large regions from only a single or a very few specimens; these areas include the Atlantic coast of South America, both coasts of Africa and the South Pacific.

If, as seems very likely, there proves to be a distinct (dwarf) form of the species in Southeast Asia, the name [*Delphinus*] *roseiventris* Wagner, 1846 may apply; the probable holotype specimen[1] MNHN 1882-104 is a small skull (condylobasal length 384 mm, zygomatic width 153 mm) from the Moluccas.

Use of the common name "Gray's spinner dolphin" is proposed for this, the nominate subspecies of *S. longirostris.*

Specimens examined.—In addition to the specimens designated as referred specimens above, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

Stenella longirostris orientalis, new subspecies

Holotype.—SDNHM 21427, physically mature male, total length 186 cm, from 12°20′N, 92°53′W (ca. 120 km off the coast

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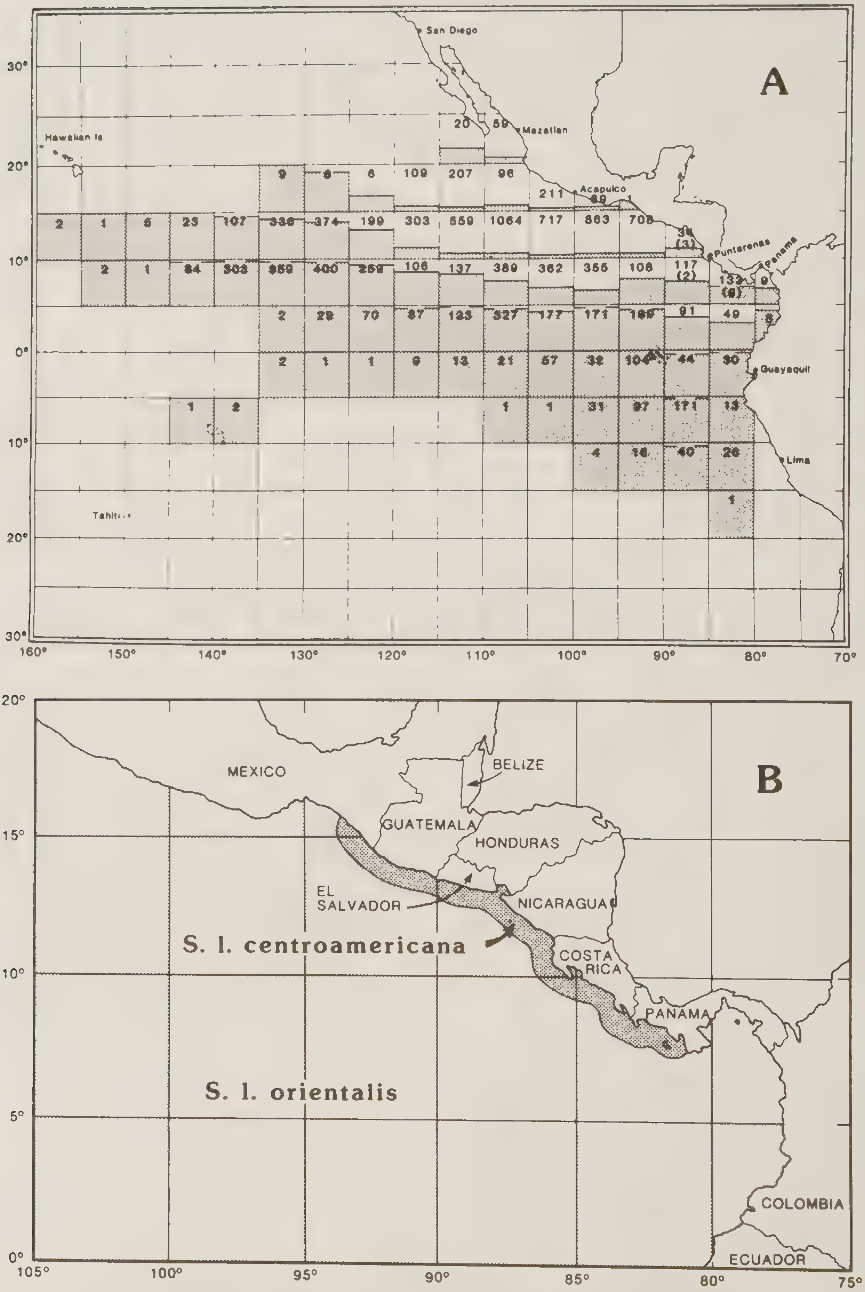
[1] The holotype specimens of Delphinidae at the MNHH are currently under review by D. Robineau of the Centre National d'Étude des Mammifères Marins.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ECUADOR
S. l. centroamericana
S. l. orientalis
20°
15°
10°
5°
0°
105°
100°
95°
90°
85°
80°
75°

Fig. 2. Distribution of subspecies of *Stenella longirostris* in the eastern Pacific. Modified from Perrin et al. (1985). A. Schools sighted from tuna seiners and research vessels, identified to subspecies on the basis of predominant appearance of dolphins in school. Numbers indicate total number of schools sighted in square. Open portion of square = proportion of total sightings in the square that were of schools of the eastern spinner, *S. l. orientalis* or (on Central American coast, listed in parentheses) *S. l. centroamericana.* Shaded portion = *S. l. longirostris* (in west, southwest, and far south) and intergrades/hybrids between *S. l. longirostris* and *S. l. orientalis.* B. Approximate distributions of *S. l. orientalis* and *S. l. centroamericana* in Central American waters, based on records with voucher specimens.

of Guatemala in the eastern tropical Pacific), 10 Mar 1968, killed incidentally in tuna purse-seine fishery, complete skeleton, cast and external photographs. External photograph in Perrin (1972:989, fig. 9) and Leatherwood et al. (1988:151, fig. 191).

Referred specimens.—USNM 395396, 395531, 39533–34 from 12°51′N, 93°18′W; USNM 395260, 395270–73, 395526, 395593, 7°11′N, 90°32′W; USNM 395274–75, SWFC 0025 (CV245), SWFC 0027 (CV240), UF18726, 7°20′N, 92°30′W; LACM 54052 (WAW50), ca. 21°16′N, 106°16′W; LACM 54036 (WAW54), ca. 18°N, 102°12′W; LACM 54039 (WAW60), 14°30′N, 99°35′W; LACM 64062 (RLB405), ca. 14°20′N, 107°20′W; USNM 324974–75, 12°32′N, 91°4′W; USNM 395930, 16°15′N, 98°55′W; CAS 15665, 13°30′ to 14°6′N, 98° to 100°56′W; CAS 15666, 13°30′ to 14°2′W, 99°47′ to 102°2′W; MVZ 140641, 13°33′ to 14°2′N, 99° to 108°W; CAS 15667–69, MVZ 140642 and 140645, UCMP 86287, 9°50′ to 10°36′N, 99°47′ to 102°2′W; USNM 395026, ca. 3°N, 87°W; USNM 396169, 7°21′N, 87°14′W; USNM 23302, Pacific Ocean between Panama and Galapagos Islands; USNM 88976, ca. 21°35′N, 106°40′W; LACM 54038 (WAW58), ca. 17°N, 100°45′W; SDMNH 21200, ca. 18°20′N, 106°40′W; CAS 13821, 13828, ca. 12°22′N, 80°50′W; MMBL 1967-102, ca. 21°43′N, 10°47′W.

Diagnosis.—A subspecies of *Stenella longirostris* characterized by uniform gray coloration dorsally and laterally (Fig. 1), with patches of white in axillary and genital areas, erect to forward-canted dorsal fin in adult male, relatively large post-anal hump, relatively small adult size (to 199 cm in adult males and 193 cm in adult females), and relatively short (351–407 mm) and narrow (zygomatic width 139–153 mm) skull.

Distribution.—Tropical coastal and oceanic waters of the eastern Pacific (Fig. 2) in a large triangular region, with the base of the triangle extending from about the tip of Baja California (ca. 24°N) in the north to ca. 10°S off the coast of Peru and the tip of the triangle at about 145°W, 10°N. Most common off Mexico and Central America, in a region extending about 1000 km offshore (Perrin et al. 1985). Replaced south of the Gulf of Tehuantepec and north of the Bay of Panama in inshore coastal waters of extreme southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua and Costa Rica by *Stenella longirostris centroamericana* (described below).

Description of holotype.—The holotype specimen, a physically mature 186-cm male (all vertebral epiphyses fused to the centra) was dark gray dorsally and laterally, with the gular region slightly lighter gray and with patches of white in the axillary and genital regions (photograph in Perrin 1972:989, fig. 9). The dorsal fin was large and canted forward, and the post-anal hump was prominent; these features are preserved in the cast of the specimen in the SDMNH collection. Measurements (in mm) of the holotype skull: condylobasal length 401, length of rostrum 259, width of rostrum at base 74, width of rostrum at ½ length 46, width of rostrum at ¾ length 33, greatest preorbital width 133, greatest postorbital width 152, zygomatic width 150, parietal width 129, length of left temporal fossa 54, height of left temporal fossa 39, length of left upper toothrow 226, length of left ramus 346, height of left ramus 54. Teeth: upper left 49, upper right 48, lower left 52, lower right 52.

Variation.—The white axillary and genital patches may be confluent, with dark spots or patches between them. In a broad zone of hybridization/intergradation with *S. l. longirostris* in the offshore eastern tropical Pacific (the range of the "whitebelly spinner"—Perrin et al. 1985), coloration may be intermediate between those of the two forms (Fig. 1; Perrin 1972, 1975a; Perrin, Sloan & Henderson 1979).

Range in total length in 431 adult males (right testis ≥100 g) was 160–199 cm (average 176.1 cm, standard deviation 6.12 cm); 697 adult females (at least one corpus in the ovaries) were 152–193 cm long (average 171.3 cm, standard deviation 5.99 cm) (Per-

Table 2.—Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected skull measurements and tooth counts for *Stenella longirostris orientalis* and *S. l. centroamericana.* From Perrin et al. (1989).

	S. l. orientalis	*S. l. centroamericana*
Condylobasal length	386.5 (26) 351–407	428.6 (5) 416–439
Length of rostrum	245.5 (26) 218–262	279.0 (5) 268–288
Width of rostrum		
At base	72.1 (29) 66–77	72.4 (5) 70–77
At ½ length	41.6 (26) 37–47	42.0 (5) 39–43
At ¾ length	30.5 (26) 26–36	29.8 (5) 28–32
Width of PMXs at ½ length	19.6 (26) 16–22	21.4 (5) 21–22
Preorbital width	132.3 (29) 127–138	134.2 (5) 131–138
Postorbital width	148.1 (29) 140–154	151.2 (5) 149–152
Zygomatic width	146.4 (29) 139–153	150.4 (5) 149–152
Parietal width	125.9 (29) 119–132	128.8 (5) 127–130
Length of temporal fossa	48.5 (29) 41–57	49.6 (5) 46–57
Height of temporal fossa	36.6 (29) 29–47	36.4 (5) 34–42
Length of upper toothrow	212.2 (25) 192–299	245.0 (5) 238–255
Length of ramus	329.1 (27) 301–348	369.6 (5) 358–379
Height of ramus	52.3 (29) 47–57	55.2 (5) 53–57
Upper teeth (per row)	52.6 ± 3.18 (32) 46–61	55.3 (5) 50–59
Lower teeth (per row)	50.5 ± 2.39 (37) 45–56	56.3 (5) 51–59

rin et al. 1985). Ranges and averages for skull measurements and tooth counts are given in Table 2.

Additional data on ontogenetic, sexual, individual and geographic variation in size, shape, coloration and skeleton are given in Perrin (1972, 1975a, b), Perrin, Sloan & Henderson (1979), Perrin et al. (1985), Schnell et al. (1982, 1985), Douglas et al. (1986), and Leatherwood et al. (1988).

Remarks.—This subspecies corresponds to the "Eastern Spinner Porpoise, *Stenella longirostris* subsp. B (unnamed?)" (Perrin 1975a). Hybrids/intergrades with *S. l. longirostris* correspond to the "Whitebelly Spinner Porpoise, *Stenella longirostris* subsp. C (unnamed?)" (Perrin 1975a).

Two alternative hypotheses have been proposed for the origin of this distinctive dolphin in the eastern Pacific: differentiation during isolation of a portion of the tropical eastern Pacific by a temperate-water barrier extending across the equator during a glacial period, or parapatric differentiation due to the peculiar oceanographic structure of the eastern Pacific (very shallow mixed layer and thick oxygen minimum layer that create an unique oceanic dolphin habitat—Au & Perryman 1985) and facilitated by complex social structure (Perrin et al. 1985).

The holotype specimen of the junior synonym *Delphinus microps* Gray, 1846 (BMNH 349a) is a small adult skull from an unknown locality; its measurements are within the range for *S. l. orientalis.* It may have come from the eastern Pacific, or it may have come from a different region where spinner dolphins are relatively small, e.g., Southeast Asia (Perrin et al. 1989). If future analyses were to determine that it came from the eastern Pacific, then the subspecies would bear the name *microps* rather than *orientalis.*

Continued use of the common name "eastern spinner dolphin" is proposed for this subspecies.

Specimens examined.—In addition to the specimens designated as referred specimens above, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

Stenella longirostris centroamericana, new subspecies

Holotype.—USNM 395933, skull and external measurements, adult male, one of three specimens collected at 9°47′N, 85°42′W (Gulf of Nicoya, Pacific coast of Costa Rica) on 26 Mar 1963 by D. W. Waller; original field number BCFBL,SD XIII-9.

Paratypes.—USNM 395931 and 395932 (same collection data as holotype).

Referred specimens.—USNM 395934 from 9°58′N, 86°3′W (outer side of Peninsula de Nicoya, Pacific coast of Costa Rica); SWFC 0025 (DAB100), 14°19′N, 93°10′W (ca. 80 km off coast of southern Mexico near border with Guatemala, at southern end of Gulf of Tehuantepec over continental shelf).

Diagnosis.—A subspecies of *Stenella longirostris* characterized by uniform gray coloration dorsally and laterally (ventral coloration poorly known, but photographs of animals in the wild and sketches by field observers do not show the well-defined axillary and genital white patches typical of *S. l. orientalis*), erect to forward-canted dorsal fin in adult male, relatively large post-anal hump, relatively large adult size (to 216 cm), and relatively long (416–439 mm) and narrow (zygomatic width 149–152 mm) skull.

Distribution.—Coastal waters to ca. 80 km offshore over the continental shelf south of the Gulf of Tehuantepec and north of the Bay of Panama off extreme southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua and Costa Rica (Fig. 2). Replaced to the north, south and west by *S. l. orientalis.*

Description of holotype.—Measurements (in mm) of the holotype skull: condylobasal length 416, length of rostrum 269, width of rostrum at base 71, width of rostrum at ½ length 43, width of rostrum at ¾ length 30, greatest preorbital width 135, greatest postorbital width 152, zygomatic width 152, parietal width 129, length of left temporal fossa 48, height of left temporal fossa 36, length of upper left toothrow 239, length of left ramus 358, height of left ramus 56. Teeth: upper left 58, upper right 57 (estimated), lower left 57, lower right 57. External measurements (taken in field by D. W. Waller, following Norris 1961, in cm) of the carcass: total length 216.4, beak tip to melon 14.3, to angle of gape 28.3, to center of eye 32.0, to blowhole 32.1, to origin of flipper 46.3, to tip of dorsal fin 100.0, to umbilicus 99.7, axillary girth 69.2, posterior length of flipper 16.8, span of flukes 39.9.

Variation.—Three adult males (testis weight ≥100 g) were 212–216 cm long and 12 adult females (at least one corpus in ovaries) 193–211 cm (average 198.8 cm) (Perrin et al. 1985). Ranges and averages for skull measurements and tooth counts are given in Table 2. Additional data on osteological variation are given in Douglas et al. (1986), Perrin (1975a, b), Perrin et al. (1985), and Schnell et al. (1982, 1985).

Remarks.—This subspecies corresponds to the "Costa Rican spinner porpoise, *Stenella longirostris* subsp. A (unnamed?)" (Perrin 1975a). It differs from *S. l. orientalis* primarily in its relatively greater body size and its relatively long and narrow skull.

The few skulls available for this form can be easily discriminated from skulls of the other forms, based on simple scatterplots of length and width measurements or on scatterplots of scores for discriminant functions (Perrin 1975a), but it can be expected that overlap will be encountered when larger series of specimens become available.

The paucity of specimens is due to an apparent ecological difference between this form and *S. l. orientalis.* Large numbers of the latter are killed by tuna purse seiners because they are captured to catch yellowfin tuna (*Thunnus albacares*) that accompany them (Perrin 1975b); the former do not often "carry fish" and thus are only very rarely captured and killed.

The common name "Costa Rican spinner

dolphin" has been used for this form since 1975, but its range is now known to include the coastal waters of several nations. Therefore it is proposed that this subspecies be called the "Central American spinner dolphin."

Specimens examined.—In addition to the specimens designated above as paratypes, the specimens listed in Perrin (1972, 1975a), Perrin, Sloan & Henderson (1979), and Perrin et al. (1981, 1989).

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Literature Cited

Au, D. W. K., & W. L. Perryman. 1985. Dolphin habitats in the eastern tropical Pacific.—Fishery Bulletin 83:623–643.

Dizon, A. E., & W. F. Perrin. 1987. Genetic distances among and within species, populations, and schools of spinner and spotted dolphins.—Abstracts of the Seventh Biennial Conference on the Biology of Marine Mammals, December 5–9, 1987, Miami, Florida, p. 17.

Douglas, M. E., G. D. Schnell, & D. J. Hough. 1986. Variation in spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific Ocean: Sexual dimorphism in cranial morphology.—Journal of Mammalogy 67:537–544.

Gilpatrick, J. W., Jr., W. F. Perrin, S. Leatherwood, & L. Shiroma. 1987. Summary of distribution records of the spinner dolphin, *Stenella longirostris*, and the pantropical spotted dolphin, *S. attenuata*, from the western Pacific Ocean, Indian Ocean and Red Sea.—U.S. Department of Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-89, 42 pp.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies.—Trends in Ecology and Evolution 3:158–167.

Leatherwood, S., R. R. Reeves, W. F. Perrin, & W. E. Evans. 1988. Whales, dolphins, and porpoises of the eastern North Pacific and adjacent Arctic waters. A guide to their identification. Dover Press, New York, 245 pp.

Norris, K. S. (ed.). 1961. Standardized methods for measuring and recording data on the smaller cetaceans.—Journal of Mammalogy 42:471–476.

Perrin, W. F. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation.—Fishery Bulletin 70:983–1003.

———. 1975a. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii.—Bulletin of the Scripps Institution of Oceanography 21:206 pp.

———. 1975b. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific.—Journal of the Fisheries Research Board of Canada 32:1059–1067.

———, & J. W. Gilpatrick, Jr. 1990. Spinner dolphin *Stenella longirostris* (Gray, 1828). *In* S. H. Ridgway & R. J. Harrison, eds., Handbook of marine mammals, volume 5. Academic Press, New York (in press).

———, W. E. Evans, & D. B. Holts. 1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76.—U.S. Department of Commerce, NOAA Technical Report, NMFS SSRF-737, 14 pp.

———, N. Miyazaki, & T. Kasuya. 1989. A dwarf form of the spinner dolphin (*Stenella longirostris*) from Thailand.—Marine Mammal Science 5:213–227.

———, P. A. Sloan, & J. R. Henderson. 1979b. Taxonomic status of the 'southwestern stocks' of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata*.—Report of the International Whaling Commission 29:175–184.

———, M. D. Scott, G. J. Walker, & V. L. Cass. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific.—U.S. Department of Commerce, NOA Technical Report, NMFS SSRF-28, 28 pp.

———, E. D. Mitchell, J. G. Mead, D. K. Caldwell, & P. J. H. van Bree. 1981. *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic.—Journal of Mammalogy 62:583–598.

———, M. D. Scott, G. J. Walker, F. M. Ralston, & D. W. K. Au. 1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, with an annotated catalog of data sources.—U.S. Department of

Commerce, NOAA Technical Memorandum, NOAA-TM-NMFS-SWFC-38, 65 pp.

Robineau, D., & J.-M. Rose. 1983. Note sur le *Stenella longirostris* (Cetacea, Delphinidae) du golfe d'Aden.—Mammalia 47:237–245.

Schnell, G. D., M. E. Douglas, & D. J. Hough. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. iongirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-82-15C, 213 pp., Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

———, ———, & ———. 1985. Further studies of morphological differentiation in spotted and spinner dolphins (*Stenella attentuata* and *S. longirostris*) from the eastern tropical Pacific. Southwest Fisheries Center Administrative Report LJ-85-04C, 30 pp., Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

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DAYTIME FEEDING BY LEACH'S STORM-PETREL ON A MIDWATER FISH IN THE EASTERN TROPICAL PACIFIC[1]

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Key words: Leach's Storm-Petrel; vertical migrators; Vinciguerria lucetia; *seabird foraging; nocturnal feeding.*

Information on the diet of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) has been obtained almost exclusively from breeding colonies where crustaceans (mainly euphausiids, but with amphipods and copepods locally important) and fish (mainly myctophids) make up the bulk of the diet (Linton 1978, Watanuki 1985, Vermeer and Devito 1988). Almost nothing is known about this species' foraging habits in the tropical

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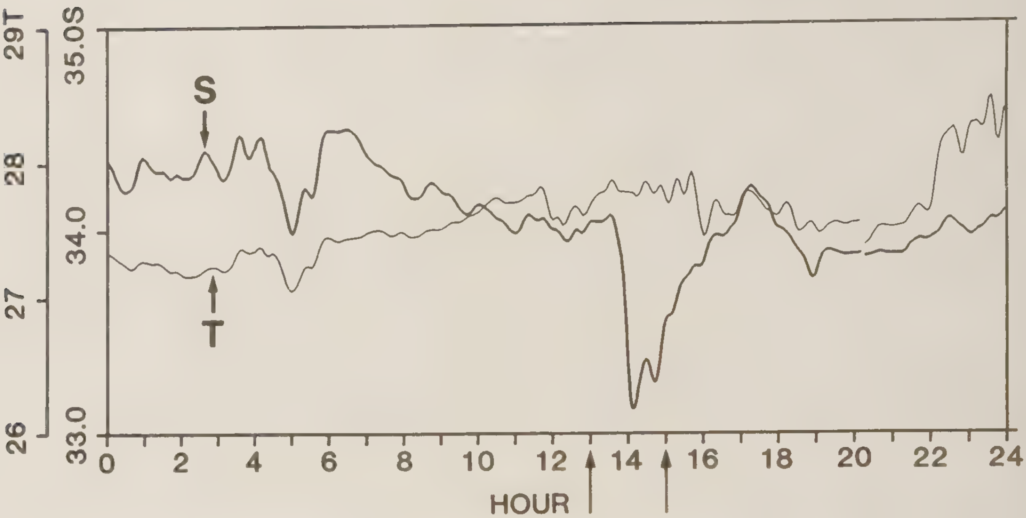

FIGURE 1. Section of strip chart showing continuous sea surface temperature (T) and salinity (S) during the day of our observation; during the time between the two arrows the ship was stopped for storm-petrel collection.

open ocean where it is commonly found during the nonbreeding season (Crossin 1974, Pitman 1986). The only reference that we know of is Ainley's (1984) comment that Leach's Storm-Petrel "feeds rather heavily" on marine insects (*Halobates* spp.) while in the tropics.

While conducting marine bird and mammal survey transects in the eastern tropical Pacific (ETP), we stopped our research vessel at approximately 13:00 LMT on 19 November 1988 at 3°44′S, 114°08′W to investigate an inordinately large concentration of storm-petrels. We had observed only small to moderate numbers of Leach's and Galapagos (*O. tethys*) storm-petrels earlier in the day (0.59/km^2 and 0.34/km^2, respectively), but in the area of concentration we saw hundreds of storm-petrels at any one time in groups of 50 to over 200. Most of the birds were sitting on the water, apparently satiated (see below), but others were in scattered flocks hovering over the water and feeding. Leach's Storm-Petrel was the predominant species though a few Galapagos Storm-Petrels were also present. One Pomarine Jaeger (*Stercorarius pomarinus*) and one White-winged Petrel (*Pterodroma leucoptera*) were the only other bird species present.

We collected six Leach's Storm-Petrels, including five from sitting groups and one bird that was actively feeding. The feeding bird was carrying a fish in its beak that was also collected. We took the specimens back to the ship and immediately examined the stomach contents.

Every bird had been feeding exclusively on a gonostomatid fish, *Vinciguerria lucetia*; stomachs were crammed with recently ingested fish as well as fish mush and otoliths. The mean weight of the six birds that we collected, to the nearest 0.5 g, less the weight of the stomach contents, was 42.0 g (range = 38.0–45.0 g); all had a light to moderate amount of subcutaneous fat. The mean weight of the stomach contents, to the nearest 0.5 g, was 8.5 g (range = 7.0–10.0 g).

Stomach contents averaged 20.4% of the body mass with a range of 15.6–24.4%. (This last mean is biased downward because one of the birds regurgitated and lost part of its stomach contents when it was collected. Also, we did not include as stomach contents the fish that was carried in the beak of the feeding bird we collected.) The range that we recorded is in close agreement with Croxall et al. (1988) who found that meal sizes for adult Wilson's Storm-Petrels (*Oceanites oceanicus*) breeding at South Georgia Island ranged from 15–25% of adult body mass. The birds that we collected appeared to have recently fed to satiation, suggesting that 25% was probably an accurate upper limit to the food-carrying capacity of Leach's Storm-Petrel (at least for a diet of fish).

In addition to the above, on 1 August 1989, at 22°43′N, 114°20′W, two separate Leach's Storm-Petrels flew onboard the authors' drifting research vessel, 45 and 90 min after dark. One regurgitated four and the other five *Vinciguerria*. The prey were half-digested and therefore were probably taken around dusk. We released the storm-petrels unharmed.

These were the first recorded instances of Leach's Storm-Petrel feeding on *Vinciguerria*. Harrison et al. (1983) found unidentified *Vinciguerria* and *V. nimbaria* to be a small but not insignificant part of the diets of nine of the 18 breeding seabirds that they studied in Hawaii; Mörzer Bruyns and Voous (1965) reported that a Sooty Tern (*Sterna fuscata*) flew aboard their ship at night in the ETP and regurgitated approximately six fairly fresh *Vinciguerria* cf. *lucetia*. We also found small numbers of *Vinciguerria* in the stomachs of Black Storm-Petrels (*Oceanodroma melania*), White-winged Petrels (*Pterodroma leucoptera*), and Juan Fernandez Petrels (*Pterodroma externa*) that were collected in the ETP during the daytime.

The storm-petrels that we collected had been taking adult *V. lucetia* that had fed recently, possibly at the surface. The abdominal area of all of the more intact fish was noticeably distended. We examined the stomach contents of a freshly caught fish dropped from the beak of the feeding storm-petrel that we collected. This fish was an adult (51 mm, standard length; Ahlstrom and Counts 1958) and was similar in size to most of the other fish that were found in the stomach samples. Its stomach was packed with freshly ingested copepods, but also contained a few euphausiid parts, an amphipod, and two fish larvae (G. Moser, pers. comm.). Diet studies on *Vinciguerria* elsewhere have found copepods to be their main prey (Shevchenko 1986, Clarke 1974).

Despite the fact that *V. lucetia* may be the most abundant and widespread fish in the ETP (Ahlstrom 1969), any daytime surface occurrence of this species is probably an unusual phenomenon. It belongs to a genus of midwater fishes known to undertake diurnal vertical migrations, and postlarval forms are rarely encountered at the surface, even at night (Clarke 1974). For example, dolphinfish, (*Coryphaena hippurus*), a large, diurnal, surface predator, occurs throughout the ETP but rarely takes *Vinciguerria* (Pitman, unpubl. notes); deeper-foraging tunas, on the other hand, prey heavily on *Vinciguerria* in the ETP (Alverson 1963; Pitman, pers. observ.).

We feel, however, that the storm-petrels that we collected were taking *Vinciguerria* which were feeding at the surface (rather than being driven there by predators from below), and we offer two lines of evidence to support this. First, most seabird flocks in the pelagic waters of the ETP form in association with tuna/dolphin aggregations because these predators often drive prey to the surface (Au and Pitman 1986). In those situations, both prey and predatory fish are regularly seen breaking the surface during their interactions and that is where foraging birds focus their attention. In the storm-petrel aggregation that is reported on here, we saw no signs of predatory fish or prey in areas where subgroups of storm-petrels were feeding. Additionally, storm-petrels do not normally join mixed-species flocks that are associated with schools of large, predatory fishes (Au and Pitman 1986).

Secondly, oceanographic data collected at the time of our observation indicated that an anomolous physical event was correlated with the observed feeding aggregation. Figure 1 shows a continuous strip chart recording of sea surface temperature and salinity for the day in question. Although the temperature remained fairly constant throughout the day, the salinity dropped precipitously (nearly 1 ppt) at approximately 13:00, when the storm-petrel concentration was noted. In the immediate area of the bird aggregation, evidence of convergent current flow at the surface was apparent to the naked eye: a thin, jagged streak of foam at least 1 km long separated flat calm water from darker, heavily rippled water. Brown (1988) discussed the importance of similar oceanographic anomolies for Leach's Storm-Petrels foraging off eastern Canada.

It appears that a local, physical oceanographic process may have served to concentrate an abundance of prey (apparently mainly copepods in this case) which attracted *Vinciguerria* to the surface. Similarly, Brown et al. (1979) reported on the daytime surface swarming in the Bay of Fundy of *Meganyctiphanes norvegica,* a vertically migrating euphausiid normally found at the surface only at night. The authors suggested that the swarms may have actively swam to the surface to prey upon copepods caught in turbulent upwelling.

Although daytime surface occurrences of diel vertical migrators like *Vinciguerria* are most likely quite rare, they can, as shown above, provide at least occasional food sources for surface feeders. Myctophids, which are also preyed upon by Leach's Storm-Petrel, are another group of vertically migrating midwater fishes normally found at the surface only at night; they have also been found on rare occasions to swarm at the surface during the daytime (Alverson 1961).

Feeding on daytime surface swarms is one of several possible ways that seabirds can feed on midwater organisms. We occasionally dipnetted Portuguese man-o-war (*Physalia*) at night that had fish caught in their tentacles, including *Vinciguerria* and myctophids. Birds that we collected in the tropics occasionally had *Physalia* tentacles draping from their beaks and it is possible that instead of eating *Physalia* they were actually stealing *Physalia* prey. We also occasionally observed Leach's Storm-Petrels feeding on dead fish and squid floating on the surface. Scavenged specimens ranged in size from over 1 m, from which birds had to tear off pieces, to smaller organisms that were swallowed whole.

These observations all indicate that care must be taken in interpreting foraging habits of seabirds based on the presumed behaviors of their prey species. For example, Linton (1978) and Vermeer and Devito (1988) studied the diets of Leach's Storm-Petrels in eastern Canada and British Columbia, respectively. Among the identified prey in both studies was a high proportion of midwater species that were vertical migrators, generally known to occur at the sea surface only at night, and from this the authors concluded that the storm-petrels had been feeding at night. Our observations suggest that some "nocturnal" prey species of Leach's Storm-Petrels also occur at least occasionally at the surface during the daytime.

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LITERATURE CITED

Ahlstrom, E. H. 1969. Mesopelagic and bathypelagic fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Rep. 13:39–44.

Ahlstrom, E. H., and R. C. Counts. 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. U.S. Fish. Wildl. Serv., Fish. Bull. 139, 58:363–416.

Ainley, D. G. 1984. Storm-petrels, p. 58–63. *In* D. Haley [ed.], Seabirds of the eastern north Pacific and arctic waters. Pacific Search Press, Seattle, WA.

Alverson, F. 1961. Daylight occurrence of myctophid fishes off the coast of Central America. Pac. Sci. 15:483.

Alverson, F. 1963. The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. Bull. Int.-Am. Trop. Tuna Comm. 7:295–396.

Au, D.W.K., and R. L. Pitman. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88:304–317.

Brown, R.G.B. 1988. The influence of oceanographic anomalies on the distributions of storm-petrels (*Hydrobatidae*) in Nova Scotian waters. Colonial Waterbirds 11:1–8.

Brown, R.G.B., S. P. Barker, and D. E. Gaskin. 1979. Daytime surface swarming by *Meganyctiphanes norvegica* (M. Sars) (Crustacea, Euphausiacea) off Brier Island, Bay of Fundy. Can. J. Zool. 57:2285–2291.

Clarke, T. A. 1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. U.S. Fish. Bull. 72:337–351.

Crossin, R. S. 1974. The storm petrels (Hydrobatidae). Smithson. Contrib. Zool. 158:154–205.

Croxall, J. P., H. J. Hill, R. Lidstone-Scott, M. J. O'Connell, and P. A. Prince. 1988. Food and feeding ecology of Wilson's storm petrel *Oceanites oceanicus* at South Georgia. J. Zool. (Lond.) 216: 83–102.

Harrison, C. S., T. S. Hida, and M. P. Seki. 1983. Hawaiian seabird feeding ecology. Wildl. Monogr. 85:1–71.

Linton, A. 1978. The food and feeding habits of the Leach's Storm-Petrel (*Oceanodroma leucorhoa*) at Pearl Island, Nova Scotia and Middle Lawn Island, Newfoundland. M.Sc.thesis, Dalhousie Univ., Halifax, Nova Scotia.

Mörzer Bruyns, W.J.F., and K. H. Voous. 1965. Night feeding by Sooty Tern (*Sterna fuscata*). Ardea 53:79.

Pitman, R. L. 1986. Atlas of seabird distribution and relative abundance in the eastern tropical Pacific. Southwest Fisheries Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, Administrative Report LJ-86-02C.

Shevchenko, N. F. 1986. Feeding of *Vinciguerria nimbaria* (Gonostomatidae) in the tropical zone of the Atlantic Ocean. J. Ichthyol. 26(4):50–56.

Vermeer, K., and K. Devito. 1988. The importance of *Paracallisoma coecus* and myctophid fishes to nesting fork-tailed and Leach's storm-petrels in the Queen Charlotte Islands, British Columbia. J. Plank. Res. 10:63–75.

Watanuki, Y. 1985. Food of breeding Leach's Storm-Petrels (*Oceanodroma leucorhoa*). Auk 102:884–886.

Application of Yield-per-Recruit and Surplus Production Models to Fishery Enhancement Through Juvenile Releases

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ABSTRACT

Yield-per-recruit and surplus production models are modified for use when hatchery-reared juveniles are released into a fishery. The yield-per-recruit model indicates that species with low ratios of natural mortality to growth and high asymptotic weight offer the greatest potential weight yield per stocked juvenile. The Ricker surplus production model is easily modified to express catches as functions of fishing effort and numbers of juveniles released. Thus the model can be used to estimate the effectiveness of stocking a fishery with hatchery releases based on a time series of catch, stocking, and effort data. The model can also be used as a simulation tool.

The release of hatchery-reared juveniles to enhance fisheries for a number of species is practiced in Japan and to a lesser degree in other countries, including the United States and Norway (Yatsuyanagi 1982, Botsford and Hobbs 1984, Isibasi 1984, Ulltang 1984). When juveniles are released to augment a natural stock that is the basis of an existing fishery, stocking combines extensive mariculture with traditional fishery science. New quantitative tools are needed to evaluate and manage this system. The simple stocking vs. harvesting ratios that are used to evaluate and manage aquaculture no longer apply in the presence of varying fishing pressure and a natural stock. For example, fishing mortality often increases as stocking levels increase, making it difficult to attribute any increase in yield solely to the increase in stocking. However, traditional fishery production models are also inadequate since they do not incorporate stocking as a variable. Although some models have been developed to examine the effects of stocking relative to hatchery cost and the return to the fishery, these analyses have not taken into account other management variables including size limits and fishing effort (e.g., Oshima 1984). More sophisticated models have been developed which can be used to simulate the effects of stocking or develop optimal fishery policy, and can be applied in situations where the biology of the resource is well known and estimates of age-specific population parameters are available (Watanabe et al. 1982, Botsford and Hobbs 1984, Ulltang 1984, Watanabe 1985).

In this paper the traditional Beverton and Holt (1957) yield-per-recruit model and the nonequilibrium Ricker surplus production model (Ludwig and Walters 1985), both standard tools for fishery management, will be modified so that they can be applied to evaluate and manage fisheries in which juveniles are released. The yield-per-recruit model can be applied with very little modification to juvenile releases to evaluate the yield-per-released-juvenile as a function of the biological parameters (growth and mortality) and management parameters (release size, size at entry, and fishing mortality). The contribution of the released juveniles to the spawning stock can be evaluated in a similar fashion by computing the spawning-stock biomass per released juvenile. The Ricker surplus production model can be modified to express the catch as a function of effort and stocking so that a time-series of stocking, catch, and effort data can be analyzed to evaluate the effectiveness of stocking and to estimate maximum sustainable yield in the presence of juvenile releases.

Yield-per-recruit models

The Beverton and Holt (1957) yield equation can be formulated as a function of the ratio of instantaneous mortality to von Bertalanffy growth (M/K), the ratio of length at recruitment to the fishery to asymptotic length (c), the ratio of fishing mortality to natural mortality (F/M), and the ratio of length of the stocked juvenile to the asymptotic length (a).

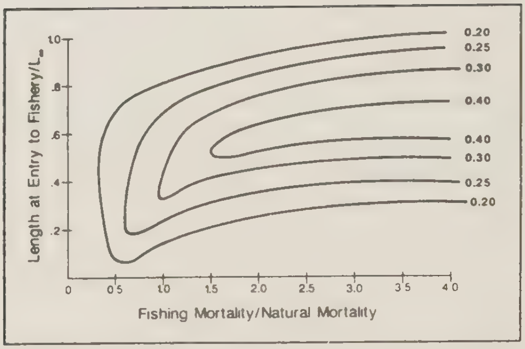

Figure 1

Yield per stocked juvenile for *Pristipomoides filamentosus* as function of relative length of entry and relative fishing mortality. Estimates of $M/K = 1.7$, $W_\infty = 8.5$ kg taken from Ralston (1981); size of release taken as $0.1\ L_\infty$.

Under this formulation the yield (Y) per stocked juveniles (S) is:

$$
\begin{aligned}
Y/S = {} & \\
& (M/K)(F/M)((1-c)/(1-a))^{(M/K)}(1/(M/K+(F/M)(M/K)) \\
& -3(1-c)/(1+(M/K)+(F/M)(M/K)) \\
& +3(1-c)^2/(2+(M/K)+(M/K)(F/M)) \\
& -(1-c)^3/(3+(M/K)+(F/M)(M/K)).
\end{aligned}
$$

In a similar fashion, the spawning-stock biomass can be expressed as a function of the same variables plus the ratio of the length at onset of sexual maturity to the asymptotic length (Beddington and Cooke 1983).

Based on these formulations, just as in the traditional yield-per-recruit analysis, the yield-per-stocked juvenile (Y/S) and the contribution of the stocked juvenile to the spawning stock biomass (SSB/S) can be calculated as functions of F/M and c (Figs. 1,2). The value of the yield per stocked juvenile varies considerably with c and F/M, so the proper choice of F/M and c is necessary to maximize the benefit from stocking. For example, in Figure 1, when the length of entry to the fishery is 50% of the asymptotic length, a hatchery-released juvenile opakapaka, *Pristipomoides filamentosus*, contributes 0.3 kg to the fishery when fishing mortality equals natural mortality; whereas when fishing mortality increases to 1.5 natural mortality, at the same size of entry, the contribution to the fishery of a hatchery-released juvenile opakapaka will increase 33% to 0.4 kg. The SSB/S isopleths indicate the contribution of a stocked juvenile to the population spawning-stock biomass. For example, for the snapper (opakapaka) when $F/M = 1.5$ and $c = 0.5$, a stocked juvenile will contribute 0.15 kg to the population spawning-stock biomass (Fig. 2). If the spawning-stock biomass of the population is known, the SSB/S equation can estimate the number of juveniles needed to be released to increase the population spawning-stock biomass to a given level. The SSB/S and Y/S equations, together with the hatchery costs and the value of the harvested fish, can serve to evaluate the economic benefits of the release programs as functions of variables c, a, M/K, and F/M.

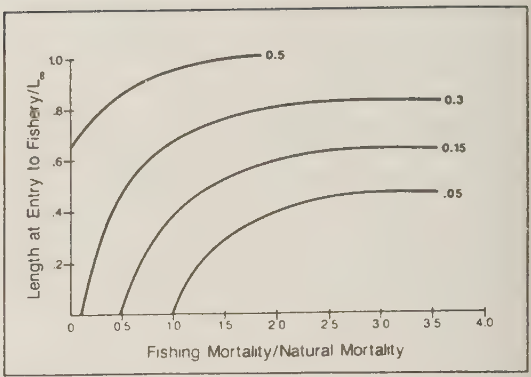

Figure 2

Spawning-stock biomass (kg) per stocked juvenile for *Pristipomoides filamentosus* as function of relative length of entry and relative fishing mortality. Estimates of $M/K = 1.7$, $W_\infty = 8.5$ kg taken from Ralston (1981); size of onset of sexual maturity taken as $0.5\ L_\infty$; size of release set at $0.1\ L_\infty$.

Hatchery technology and knowledge of the early-life history of marine organisms have made it possible to rear numerous marine organisms. The Y/S and SSB/S equations permit comparisons of the benefits from stocking among species with different population parameters. For example, there are three commercially important species in Hawaii that might be candidates for hatchery release programs: Mahimahi, *Coryphaena hippurus*; a snapper, *P. filamentosus*; and a spiny lobster, *Panulirus marginatus*. The Y/S isopleths were computed for each of these species, and the maximum values of Y/S, for all c, as a function of F/M, were determined. These maximum values of Y/S are plotted for the three species (Fig. 3). The differences between the three species in their contribution to the fishery are striking. For example, when fishing mortality is equal to natural mortality and the size at entry to the fishery is optimal, a released spiny lobster will contribute 0.02 kg to the fishery, a released snapper will contribute 0.3 kg, and a released mahimahi will contribute an amazing 2.5 kg. Even when price per kilogram is considered and the possibility that only 25-50% of adult mahimahi remain around the islands, the mahimahi releases appear to offer high economic return. The contribution of a released mahimahi to the fishery is so much greater than that of the snapper, and in turn the contribution of a snapper is greater than that of the spiny lobster, largely because of differences in the M/K ratio (1.0 for mahimahi, 1.7 for snapper, and 3.0 for lobster) and the asymptotic weight (30 kg for mahimahi, 8.5 kg for snapper, and 1.7 kg for spiny lobster). The lower the ratio of natural mortality to growth, the greater the survival of the released individual; and the

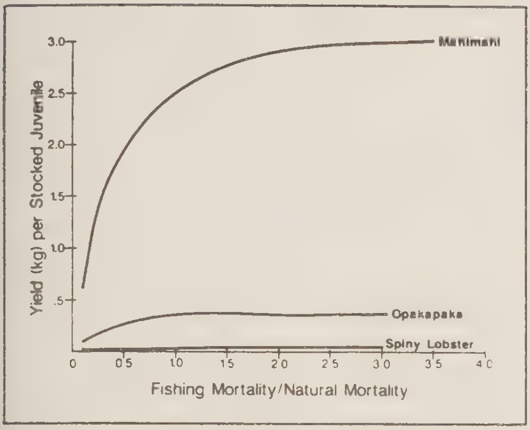

Figure 3

Maximum yield per stocked juvenile as a function of relative fishing mortality for mahimahi, opakapaka, and spiny lobster. Parameter estimates for mahimahi $M/K = 1.0$, $W = 30$ kg (Uchiyama et al. 1986); for opakapaka $M/K = 1.7$, $W = 8.5$ kg (Ralston 1981); for spiny lobster $M/K = 3.0$, $W = 1.7$ kg (Polovina unpubl. data).

greater the asymptotic weight, the greater the weight gained by the released individual. The SSB/S follows the same order for the three species as Y/S. Thus among the candidates for juvenile release, those with low M/K ratios and high asymptotic weights will offer the greatest contribution in biomass to the fishery.

Fishery production models with stocking

The most frequently used production models, Schaefer and Gulland-Fox, do not explicitly specify a recruitment relationship, and hence do not easily lend themselves to modification to include hatchery releases. However, the Ricker model for surplus production (Ludwig and Hilborn 1983) is a simple production model which can easily handle stocking. The Ricker model for surplus production is expressed by the following three equations (Ludwig and Walters 1985):

$$B_{t+1} = S_t \exp(A - BS_t + U_t) \qquad (1)$$

$$S_t = B_t - C_t \qquad (2)$$

$$C_t = B_t(1 - \exp(-qE_t)) \qquad (3)$$

where B_t is the population biomass in year t, S_t is the biomass remaining after harvest in year t, C_t represents the catch in year t, E_t denotes the effort in year t, U_t represents independent normally distributed random variables with mean 0 and variance v, and A, B, and q are parameters estimated from catch and effort data.

To modify these equations to include H_t hatchery-released juveniles in year t before harvesting, it is necessary to express the biomass in year $t+1$ resulting from H_t. A power function relationship

$$B_{t+1} = a(H_t)^b$$

with parameters a and b appears appropriate for hatchery releases of Oregon coho salmon (Peterman and Routledge 1983). For a fast-growing species the major contribution from stocking to the fishable biomass will occur in the same year as the stocking, and thus H_{t+1} rather than H_t would be used in the power function equation.

If the biomass from the hatchery-released stock is simply added to that of the natural stock in the first equation of the Ricker model for surplus production, then we obtain:

$$B_{t+1} = S_t \exp(A - BS_t + U_t) + a(H_t)^b. \qquad (4)$$

This modified equation, together with the two other equations of the Ricker model, produces a production model which incorporates hatchery releases. The contribution of the hatchery releases will increase the catch directly through Equation (3) and those that are not caught will increase S_t through Equation (2).

The Ricker surplus model without stocking shows the usual dome shape in which production first increases then decreases ultimately to zero with increasing fishing mortality (Fig. 4). When a fixed number of hatchery releases are added to the system, the yield curve has the usual dome shape as a function of fishing mortality; but rather than declining to zero, as is the case of an unstocked population, the yield approaches an asymptotic yield of $a(H_t)^b$ with increasing fishing mortality (Fig. 4). The relative contribution of the releases to the fishery will be greatest for relatively high levels of fishing mortality. Hatchery releases can increase the maximum yield and the corresponding level of optimum fishing effort.

If hatchery releases occur in the absence of a natural population the Ricker model with stocking just reduces one equation:

$$C_t = a(H_t)^b \ (1 - \exp(-qE_t)).$$

Unfortunately, due to the nonlinear nature of the Ricker surplus production model, it is not as easy to estimate the parameters as, for example, for the Schaefer model. A complete approach to parameter estimation for the Ricker model is presented in Ludwig and Hilborn (1983). Here a simplified approach will be presented for the Ricker model with stocking when it is assumed that the fishing effort is measured without error. First, assume a value for q and compute B_t and C_t from Equations (2) and (3). Then estimate A, B, a, and b from Equation (4) with the nonlinear regression, using the B's and S's obtained from the previous step. Finally, vary q and repeat the previous steps until the sums of squares of the nonlinear regression are minimized. Computer programs for nonlinear regression can typically be used as a basis for this parameter estimation approach.

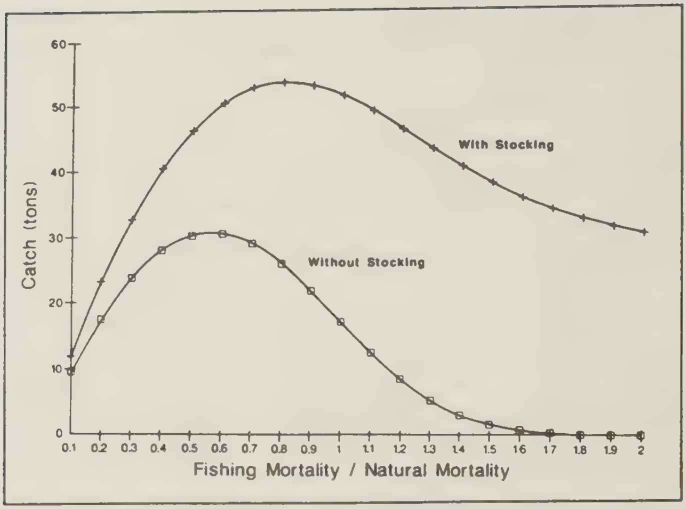

Figure 4

Equilibrium Ricker surplus production model with and without stocking. Curve without stocking based on biomass model $B = S\ \exp(0.7 - 0.007S)$; curve with stocking based on $B = S\ \exp(0.7 - 007S) + 25$.

An experimental approach to stocking can be an efficient means of evaluating the effectiveness of stocking and identifying optimal stocking levels, but simulation of any design is a necessary first step before implementation. For example, releasing juveniles into a fishery on alternating years and then comparing catches in years *with* stocking to catches in years *without* stocking may be considered a way to estimate the effectiveness of stocking. This experimental design can be simulated with the stocking surplus production model (Fig. 5). Suppose a population has a carrying-capacity biomass of 100 t and is fished with a fishing mortality of $F = 1.0$. Suppose juveniles are released in a quantity which contributes 20 t to the fishable biomass over a 10-year period on years 2, 4, 6, 8, and 10, and no releases occur in years 1, 3, 5, 7, and 9. The stocking surplus production model estimates that equilibrium fishing with $F = 1.0$ results in a catch of about 49 t annually. The first stocking (year 2) increases the catch to 62 t, and then the catch follows an oscillating sequence of lower catches during years *without* stocking and higher catches during years *with* stocking. The oscillating sequence has an increasing trend over time as the stock biomass grows due to stocking. At some point an equilibrium would be reached and the sequence would oscillate between the same two levels of catch. However, the use of this design to estimate the effectiveness of stocking by comparing catches between years with and without stocking would underestimate the effectiveness of stocking at this level of fishing mortality, since the catches do not return to their prestocking level between years of stocking.

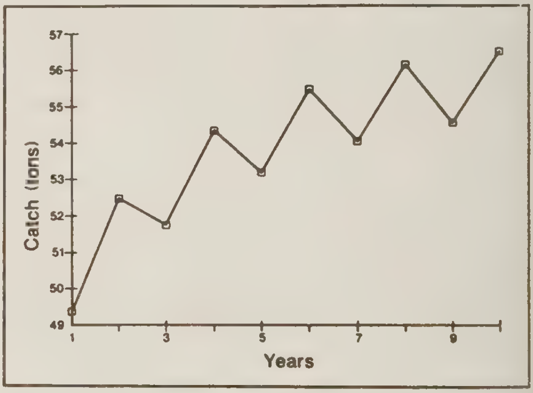

Figure 5

Simulation of yield with $F = 1.0$ when stocking occurs on even numbered years. Parameters of the Ricker surplus production model with stocking are: $A = 1.2$, $B = 0.007$, $a(H_t)^b = 20t$.

Citations

Beddington, J.R., and J.G. Cooke
1983 The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

Beverton, R.J.H., and S.J. Holt
1957 On the dynamics of exploited fish populations. Fish. Invest. Ser. II Mar. Fish. G.B. Minist. Agric. Fish. Food 19, 533 p.

Botsford, L.W., and R.C. Hobbs
1984 Optimal fishery policy with artificial enhancement through stocking: California's white sturgeon as an example. Ecol. Model. 23: 293-312.

Isibasi, K.
1984 A statistical assessment on the effect of liberation of larvae in the sea-farming—I. On the effect of liberation in the case of Kuruma prawn (*Penaeus japonicus*). Bull. Tokai Reg. Fish. Res. Lab. 113: 141-155.

Ludwig, D., and R. Hilborn
1983 Adaptive probing strategies for age-structured fish stocks. Can. J. Fish. Aquat. Sci. 40:559-569.

Ludwig, D., and C.J. Walters
1985 Are age-structured models appropriate for catch-effort data? Can. J. Fish. Aquat. Sci. 42:1066-1072.

Oshima, Y.
1984 Status of fish farming and related technological development in the cultivation of aquatic resources in Japan. *In* Liao, I.C., and R. Hirano (eds.), Proceedings of ROC-JAPAN Symposium on Mariculture, p. 1-11. TML Conference Proceedings 1, Tungkang Mar. Lab., Tungkang, Pingtung, Taiwan, R.O.C.

Peterman, R.M., and R.D. Routledge
1983 Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): Designing for yield of information. Can. J. Fish. Aquat. Sci. 40:1212-1223.

Ralston S.
1981 A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus*. Ph.D. Diss., Univ. Wash., Seattle, 204 p.

Uchiyama, J.H., R.K. Burch, and S.A. Kraul
1986 Growth of dolphins, *Coryphaena hippurus* and *C. equiselis*, in Hawaiian waters as determined by daily increments on otoliths. Fish. Bull., U.S. 84:186-191.

Ulltang, Ø.
1984 The management of cod stocks with special reference to growth and recruitment overfishing and the question whether artificial propagation can help to solve management problems. *In* Dahl, E., et al. (eds.), The propagation of cod *Gadus morhua* L., p. 795-817. Flødevigen, rapp. 1.

Watanabe, S.
1985 Restocking effects on the two competing species system, including a nonlinear regulated species population. J. Tokyo Univ. Fish. 72(2):57-63.

Watanabe, S., R. Matsunaga, and H. Fushimi
1982 Age-structured matrix model including catch and restocking. J. Tokyo Univ. Fish. 68(1-2):15-23.

Yatsuyanagi, K.
1982 Productive effect in stocking of prawn seedling in water adjacent to Yamaguchi Pref. and Suho-Nada. Bull. Yamaguchi Prefect. Naikai Fish. Exp. Stn. 10, 52 p. [in Jpn.].

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INTRODUCTION AND SUMMARY OF METHODS AND RESULTS FROM THE TROPICAL STOCK ASSESSMENT WORKSHOP

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A 3-week workshop was convened to assist fishery scientists from selected Pacific island countries in analyzing their research and commercial catch and effort data on deepwater snappers. Workshop participants came from the Cook Islands, Fiji, Kingdom of Tonga, Papua New Guinea, Solomon Islands, Tuvalu, Vanuatu, and Western Samoa. The ultimate objectives of the analyses were to estimate the maximum sustainable yield (MSY) and the fishing effort that achieves the MSY for deepwater snappers in each country. As a simplifying step, all analyses treated this multispecies resource as a single group by combining all species.

Since the deepwater snapper fisheries in all of the Pacific islands represented at the workshop are undeveloped or very recently developed, no long-term time series of catch and effort data are available to apply to production models. An alternate approach estimates unexploited exploitable standing stock (N_0) from the depletion of an area, typically a small seamount or island, and then estimates MSY as a fraction of the unexploited exploitable biomass (B_0; Polovina and Ralston 1986). To estimate N_0 from a depletion or intensive fishing study, two analytical models are used. If the depletion has occurred during a short time period so that the number of fish added by recruitment or removed by natural mortality is a minimal part of the population, then the Leslie model (Ricker 1975) is used. This model estimates catchability (q) and N_0 by regressing catch (expressed in numbers of fish) per unit effort (CPUE), against the cumulative number of fish caught. However, if the period covered by the depletion is long enough so that recruitment and natural mortality may have a significant impact on the population, then the Allen model (Sainsbury 1984) is used to estimate catchability (q) and N_0. The Allen model requires an estimate of natural mortality (M); it estimates q and mean recruitment (R) by regressing catch on two variables: effort and the product of effort with adjusted cumulative catch. Generally when the period covered by the depletion study is less than 9 months, then the Leslie model is used; when the period exceeds 9 months, then the Allen model is used. For the depletion and MSY analyses, whenever an estimate of M is required, two values ($M = 0.25$/year and 0.50/year) are used to represent a range from the published literature on deepwater snappers (Ralston 1987).

Once estimates of N_0 are obtained from either the Leslie or Allen model, they are adjusted for the habitat area of the depletion site by dividing N_0 by the length (in nautical miles) of the 200 m isobath. The estimates of N_0 are converted to B_0 by multiplying N_0 by mean fish weight.

Estimates of MSY are computed with three approaches: the Gulland method, which estimates MSY as $0.5MB_0$; the Pauly method, which estimates MSY as $2.3(w)^{-0.26}$, where w is the mean (in grams) of the asymptotic weight and the weight at the onset of sexual maturity (Pauly 1983); and a method based on the Beverton-Holt equation in which MSY is estimated as a fraction of B_0 with the fraction as a function of parameters, including M/K, where K is the von Bertalanffy growth constant, and age at recruitment to the fishery (t_r) (Beddington and Cooke 1983). The parameter M/K is estimated at 2.0, based on estimates for M and K for deepwater snappers from the literature (Ralston 1987). The estimated age at recruitment to the fishery is 3 years for Vanuatu and 4 years for all of the other study areas. For each country, an MSY estimate is computed as the product of the MSY range per nautical mile of 200 m isobath and the total length of the 200 m isobath.

Fishing mortality (F) is estimated from catchability, which is estimated from the depletion analyses for each country. The value of q from each depletion analysis is multiplied by the length of 200 m isobath to obtain a standardized q. The mean of all standardized q values from within a country is multiplied by the total fishing effort and then divided by the total length of the 200 m isobath to estimate annual F, which can be interpreted: When F equals M, then fishing effort is optimal to produce MSY; when F exceeds M, then fishing effort is excessive.

The results of 18 depletion analyses from the workshop are presented in Table 1. Table 2 presents a summary of the estimated unexploited exploitable biomass per nautical mile of 200 m isobath from the depletion analyses by seamount and island grouping. Except for a few outliers, most estimates of B_0 cluster around the median values of 2.7 metric tons (t)/nmi for seamounts and 0.7 t/nmi for islands. Since the seamounts are smaller than the islands and have a steeper slope, the difference in the estimates of B_0/nmi between seamounts and islands may, to some extent, be due to the concentration of biomass over the smaller habitat areas available at seamounts.

The ratios of MSY to B_0 by the Beverton and Holt, Gulland, and Pauly models have a range of about 10 to 30% (Table 3). For an M of 0.25, based on the Gulland estimate, a lower bound of MSY estimated at 9% B_0 is obtained. Conversely, using the Beverton and Holt equation and an M of 0.5 or using the Pauly method, which depends only on fish weight, estimates MSY at about 30% B_0. Thus, the range of 10 to 30% B_0 is estimated to include the true value of MSY.

Table 4 presents the MSY estimate for each country. For Tonga, current landings from the seamounts are almost twice the upper bound of the estimated MSY, and F is about equal to M. This result suggests that fishing effort is at the level which produces MSY and, once the fishery at the seamounts reaches its equilibrium level, the catches and CPUE will be substantially lower. However, if new seamounts are found, the higher catches may be sustained for a longer time. In Western Samoa, the

Table 1. Summary of results of depletion analyses

COUNTRY Area	Type	Principal Species	Nautical Miles of 200 meter Isobaths	(Method) Number of Fish / nml		Fish Mean Wgt (Kg.)	Unexploited Biomass / nml (Tonnes)		Recruitment R/nml/year	
MARIANAS		Pristipomoides zonatus		(Leslie)			(Leslie)			
Pathfinder Reef	Seamount	P. auricilla	3.00	1354		1.5	2.0			
		P. flavipinnis								
		Etelis carbunculus								
TONGA		P. filamentosus		(Allen)			(Allen)		(Number of fish)	
		P. flavipinnis		M=.25	M=.50		M=.25	M=.50	M=.25	M=.50
801	Seamount	Etelis coruscans	5.00	616	554	4.4	2.7	2.4	197	344
901	Seamount	E. carbunculus	6.80	614	351	4.4	2.7	1.5	137	202
903	Seamount		35.00	547	608	4.4	2.4	2.7	118	265
1004	Seamount		1.20	1927	1233	4.4	8.5	5.4	493	762
FIJI SEAMOUNTS		Etelis coruscans		(Leslie)			(Leslie)			
Taveuni	Seamount	E. carbunculus	3.10	333		7.5		2.5		
Napuka	Seamount		4.20	507		7.5		3.8		
Kadavu	Seamount		18.00	200		7.5		1.5		
Savusavu	Seamount		7.90	189		6.5		1.2		
GRID 147	Seamount		13,10	931		7.5		7.0		
FIJI SHELF										
Nasilai to Ovalau	Island		50.00	94		7.5		0.7		
Ovalau to MoonReef	Island		42.00	95		7.5		0.7		
MoonReef to Ellington	Island		40.00	75		7.5		0.6		
GRID 482	Island		40.00	73		7.5		0.5		
VANUATU									Recruitment R/nml/year - tonne	
		Etelis carbunculus		(Allen)			(Allen)			
		E. coruscans		M=.25	M=.50		M=.25	M=.50	M=.25	M=.50
Paama	Island	E. radiosus	28.00	1277	1100	1.8	2.3	1.1	0.30	0.37
Ambae	Island	Lutjanus malabarius	62.00	389	167	1.8	0.7	0.3	0.10	0.13
PAPUA NEW GUINEA		P. multidens		(Leslie)			(Leslie)			
Schoutten Islands	Island	P. filamentosus	33.00	121		2		0.2		
Kavieng	Seamount	E. carbunculus	0.25	416		2		3.3		
		Wattsia mosambitus								
		L. malabaricus								
		Paracaesio stonei								

Table 2. Length of 200m isobaths and Bo/nmi of 200m isobath for all depletion analyses

	Nautical Miles	Unexploited Biomass / nmi.
SEAMOUNTS		
Kavieng	0.25	3.30
1004	1.20	8.50
Pathfinder	3.00	2.00
Tavenui	3.10	2.50
Napuka	4.20	3.80
801	5.00	2.70
901	6.80	2.70
Savusavu	7.90	1.40
GRID 147	13.10	7.00
Kadavu	18.00	1.50
903	35.00	2.40
		2.70 = Median
ISLAND		
Paama	28.00	2.30
Schoutten Islands	33.00	0.20
MoonReef to Ellington	40.00	0.60
GRID 482	40.00	0.55
Ovalau to MoonReef	42.00	0.70
Nasilai to Ovalau	50.00	0.70
Ambae	62.00	0.70
		0.70 = Median

Table 3. Ratios of MSY to Bo for the three methods

	MSY/B M=.25	MSY/B M=.5
Gulland (1/2m)	0.13	0.25
Beverton-Holt when m/k = 2		
age at recruitment = 3 years	0.06	0.18
age at recruitment = 4 years	0.09	0.28
Pauly (2.3w)^-.26		
Marianas	0.34	
Papua New Guinea	0.28	
Western Samoa	0.27	
Vanuatu	0.32	
Tonga	0.28	

Table 4. Estimates of MSY, 1988 Landings, and F for deepwater snappers at selected Pacific island countries

COUNTRY	Estimated MSY (Tons/yr)	1988 Landings (Tons/yr)	1988 Estimated F (fishing mortality per year
TONGA	77 - 222	391	0.38
WESTERN SAMOA	17 - 50	25	(*)
FIJI current fishing area of 500 nmi of 200m habitat now being fished	70 - 200	300	0.12
FIJI potential fishing area of 3000 nmi	426 - 1280	0	0
PAPUA NEW GUINEA	170 - 270	0	0
VANUATU	113 - 190	40	.07

(*) No estimate of q available to estimate F deepwater snapper resource is already close to MSY, but some increase is possible. The fishery in Fiji is currently fishing only about 20% of the estimated 3,000 nmi of 200 m isobath. Thus, Fiji has the potential to increase catches if this unfished habitat has populations of deepwater snappers. However, if the fishery remains only within the habitat currently fished, catches will decline perhaps by 50%. The level of fishing effort may be a little lower than the level which produces MSY. Papua New Guinea has no appreciable landings of deepwater snappers, but a potential exists with MSY in the range of 170 to 270 t/year. Vanuatu's landings represent only one-third to one-fifth of the potential MSY, as indicated by the current landings and level of *F*; therefore, the potential exists for greater landings.

A point worth emphasizing is that the results from this workshop represent preliminary estimates of future MSY based on estimates of unexploited biomass and certain mathematical models that project the response of the populations to exploitation. The MSY estimates represent a sustainable equilibrium level, which is lower than the catches that can be obtained in the early stages of the fishery. As the fishery in each country develops, these preliminary estimates of MSY can be improved from a time series of catch and fishing effort data recorded by island.

This workshop also examined the utility of length-frequency data to estimate relative fishing mortality but found that size-frequency samples from the commercial catches do not provide very accurate indicators of fishing mortality, perhaps because of fish size and depth relationships and size-specific targeting by fishermen.

Finally, this workshop focused on the dynamics of the resource and did not consider the dynamics of the fishing operations. In some countries, market conditions and economics of other fisheries may limit fishing for deepwater snappers so that the MSY level is not achieved. In other instances, the distances from port to some of the deepwater snapper grounds may also limit fishing effort below the level resulting in MSY.

CITATIONS

Beddington, J. R., and J. G. Cooke.
1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.

Pauly, D.
1983. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. 234, 52 p.

Polovina, J. J., and S. Ralston.
1986. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. Fish. Bull., U.S. 84:759-770.

Ralston, S.
1987. Mortality rates of snappers and groupers. Pages 375-404 *in* J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: biology and fishery management. Westview Press, Boulder.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Sainsbury, K. J.
1984. Optimal mesh size for tropical multispecies trawl fisheries. J. Cons. int. Explor. Mer 41:129-139.

9049

LIMITED ENTRY AND HAWAII'S FISHERIES INTERACTION PROBLEM

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ABSTRACT[1]

Limited entry alone offers little solace for a fishery faced with discards or bycatch. Limited entry schemes may intensify discard problems in multispecies or multipurpose fisheries. Discards and bycatch, particularly in a multipurpose fishery, may weaken limited entry schemes. However, limited entry may reduce the scope of the discards or bycatch regulatory problem. As a result, the problem of limited entry as an economist's solution to fishery problems may be reduced. Limited entry should not be viewed as generating a single optimum solution (frequently viewed as monopolistic), but as contributing to a multi-sided solution to a multi-sided problem.

Limited entry initially was promoted because of two salient observations: (1) unrestricted access to a fishery results in biological and economic depression; and (2) direct regulations on the operations of individual harvesting firms (i.e., quotas, area and gear restrictions, etc.) provide one-sided constraints on production (i.e., they are inefficient).[2] Limited entry provides the advantage of restricting an easily quantifiable input (number of vessels) and thus provides a constraint on fishing effort without restricting actual fishing practices. Unfortunately, regulation of bycatch or discards is a form of direct regulation, since output taxes have not been considered in U.S. fisheries. Interestingly, McConnell and Norton identified bycatch in a limited entry system oriented toward a multispecies fishery (an ecosystem basis) as a major problem. Therefore, the problem is to adjust limited entry schemes to account for the joint production nature of the discards or bycatch fisheries.

Managers have used limited entry primarily in fisheries where bycatch is not a major problem. However, in its current application in Northwestern Hawaiian Islands bottomfish and its proposed application to main Hawaiian Islands pelagics (tunas and billfish), bycatch can be a major portion of the production.

One should view limited entry in these situations as placing a general

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[1] A transcript of the complete presentation is available from the author.

[2] McConnell, K. E. and V. J. Norton. 1980. An Evaluation of Limited Entry and Alternative Fishery Management Schemes. In: *Limited Entry as a Fishery Management Tool*. R. B. Rettig and J. J. C. Ginter, editors. Seattle: University of Washington Press.

limit on overall productive capacity, probably in an operating environment of multispecies and multipurpose fisheries, rather than solving the problem or providing a single point optimum. Alternative management measures should be devised to deal with the joint production problems.

9050

Size Selection of Snappers (*Lutjanidae*) by Hook and Line Gear

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The most commonly used theoretical models of gear selection have been the logistic and normal curves. These are usually applied to trawls and gillnets, respectively. In contrast, little critical work has been completed concerning the selective properties of fish hooks, although both types of selectivity curves have arbitrarily been applied to hook catch data in the literature. No study has clearly demonstrated the actual form of a selection curve for hooks. To determine which type of curve (logistic or normal) best describes the selective sampling characteristics of fish hooks, an experiment was conducted in the Marianas Islands during 1982–84. During all fishing operations two different sizes (#20 and #28) of circle fish hooks were fished simultaneously and in equal number. Under these conditions, the length specific ratios of snapper (*Lutjanidae*) catches taken by the two hook sizes provided a basis for distinguishing which model was most appropriate. Results showed that neither model in its simplest form depicted hook selectivity well. While small hooks caught substantially more small fish, large hooks were somewhat more effective in capturing the larger size classes.

Les modèles théoriques de la sélectivité des engins les plus couramment utilisés sont les courbes logistiques et normales, qui sont généralement appliquées respectivement aux chaluts et aux filets maillants. On a par contre effectué très peu d'études critiques sur les propriétés sélectives des hameçons, bien que les deux types de courbes de sélectivité aient été arbitrairement appliquées dans certaines travaux aux données concernant les prises faites à l'hameçon. Aucune étude n'a clairement démontré la forme réelle d'une courbe de sélectivité des hameçons. Pour déterminer quel type de courbe (logistique ou normale) décrit le mieux les caractéristiques de prélèvement des hameçons, nous avons mené entre 1982 et 1984 une expérience aux îles Mariannes. Pendant toutes les opérations de pêche, on a utilisé des hameçons circulaires de deux tailles différentes (n° 20 et n° 28) simultanément et en nombre égal. Dans ces conditions, le rapport de longueur des captures de vivaneaux (Lutjanidés) effectuées avec les deux hameçons a servi de base pour déterminer quel modèle convenait le mieux. Les résultats ont montré qu'aucun des modèles sous sa forme la plus simiple ne décrivait correctement la sélectivité des hameçons. Tandis que les petits hameçons capturaient nettement plus de poisson de petite taille, les gros hameçons étaient légèrement plus efficaces pour la capture des classes de taille supérieure.

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Many of the world's most important fisheries use hook-and-line gear. Examples include the Japanese, Korean, and Taiwanese distant-water longline fisheries for tuna (Brock 1962), the west coast salmon troll fishery, and the groundline fishery for Pacific halibut (Myhre and Quinn 1984). Likewise, all recreational pole-and-line fisheries, both marine and freshwater, are based on angling with fish hooks. However, despite this widespread use, the sampling characteristics of hook-and-line gear are not well understood. There has been no coherent development of theory concerning the manner in which fish hooks sample a population (Clark 1960; Pope et al. 1975). As a result, it is difficult, if not impossible, to deduce the age or size structure of a population from a single hook-and-line catch sample. One reason for this is that gear selection models developed for trawl and gillnet fisheries have been applied to hook-and-line based fisheries with little or no verification that these models are, under a broad range of conditions, well-suited to the task (e.g. Koike and Kanda 1978; Munro 1983).

One of the earliest works on hook selection showed that length–frequency samples of cod caught with longline gear were shifted to smaller sizes than similar samples that were taken with purse seine gear. The latter gear type was believed to representatively sample the population's size structure (Rollefsen 1953), suggesting that the selectivity curve for hooks must ultimately decrease with increasing size of fish. Such a pattern is in some ways similar to selection curves for gillnets, which show rising and falling limbs. Gillnet selectivity has usually been described with the symmetrical normal curve (Hamley 1975). Other studies have shown similar results from hook-and-line fishing (haddock in McCracken 1963; Koike et al. 1968; Goose Islands halibut in Myhre 1969; Takeuchi and Koike 1969; Kanda et al. 1978; Koike and Kanda 1978; Leclerc and Power 1980). However, in most of these studies the righthand "descending" limb of the selection curve was ill-defined due to sample size limitations.

In contrast, some investigators have been unable to show a decline in the righthand limb of hook selection curves, suggesting something akin to the asymptotic logistic selectivity of trawl gear (Pope et al. 1975). In particular, length–frequency samples of cod studied by McCracken (1963) and Saetersdal (1963) showed: (1) no difference from trawl catch size structure

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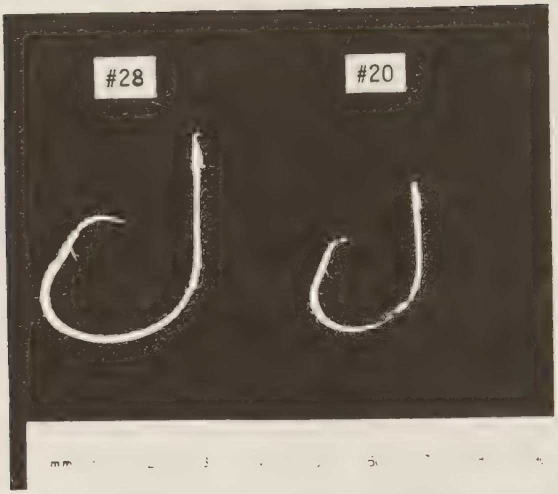

FIG. 1. The two sizes of Izuo circle fish hooks used during comparative fishing trials in the Marianas archipelago from 1982–84.

and (2) no effect of changing hook size on the catch of medium-large sized fish. Comparable findings were also reported for halibut by Myhre (1969); Ralston (1982); and Bertrand (1988).

The purpose of this study was, therefore, to perform a comparative fishing experiment (sensu Margetts 1969) with the goal of evaluating the efficacy of the logistic and normal selection models in describing patterns of hook selectivity.

Methods

As part of a multispecies resource assessment (Polovina and Ralston 1986), deepwater (100–300 m) fishing with hook-and-line gear was conducted throughout the Mariana Islands (lat. 13–20°N, long. 143–146°E) from April 1982 to May 1984. During this time six 40-d cruises were completed, with the waters surrounding all the islands of the archipelago sampled at least once, and some as many as six times (Polovina 1986). Fishing activity was directed toward the assemblage of eteline snappers (Lutjanidae), groupers (Epinephelinae), and jacks (Carangidae) that characteristically occupy deep reef habitats throughout the tropical Indo-Pacific (Forster 1984; Ralston et al. 1986).

Sampling was done from the R/V *Townsend Cromwell* while drift fishing with four hand-operated hydraulic fishing gurdies, each outfitted with ~365 m of braided prestretched Dacron line. The terminal rig was equipped with four Izuo[2] circle fish hooks (Forster 1973) attached by 60-cm gangions to the main line, which was weighted with a 2-kg iron bar. The two forward fishing lines on the vessel were equipped exclusively with #20 hooks, while the two aft lines only used #28 hooks (Fig. 1). Baits were pieces of uniformly cut stripped squid that were randomly allocated to each rig. Overall, the type and configuration of the fishing gear was similar to that employed commercially.

During fishing operations all four lines were fished concurrently so that at any point in time equal numbers (eight) of the two sizes of hooks were in use. All fish that were landed were classified by hook size of capture, identified to species, measured to the nearest millimetre fork length (FL), and weighed to the nearest 0.01 kg. Data were summarized for each species and hook size combination by rounding FL to the nearest 20 mm and aggregating the data into length–frequency distributions.

Evaluating Competing Models of Gear Selection

It is useful to draw a distinction between the intrinsic selective properties of a fishing gear and other aspects of "selectivity" extrinsic to the gear (Clark 1960). For example, year-to-year changes in the availability of a stock contribute to the latter. Likewise, selection curves obtained from cohort, virtual population, or catch-at-age analysis represent the combined effects of intrinsic and extrinsic selection factors. However, in this paper I refer to selectivity in the narrower, intrinsic sense, i.e., the size-specific likelihood of capture once a fish has encountered the gear. Selection coefficients are scaled to the fish size caught most readily and, therefore, range from 0.00–1.00. Thus, selection curves can be characterized for specific gear types, irrespective of changes in the distribution or behavior of the fish.

A more explicit quantitative definition of selectivity is provided by the relationship:

$$(1)\quad C_{i,j} = s_{i,j}\, q_i f_i N_j$$

where $C_{i,j}$ is the catch in numbers of fish in size class j on some fishing gear of size i; $s_{i,j}$ is the selection coefficient of gear size i to fish size j; q_i is the full selection ($s_{i,j} = 1.00$) catchability coefficient of gear size i; f_i is the amount of fishing effort with gear size i; and N_j is the number of fish in the population of size j (based on Hamley 1975).

A standard gear selection curve shows the relationship between the selection coefficient on the ordinate and fish size on the abscissa (Type A curve sensu Regier and Robson 1966). While there are a number of ways in which to estimate the shape of a selection curve, direct determination (Pope et al. 1975) is best. Unfortunately, there are few such studies in the literature, especially for hooks, because the size structure of the sampled population must be accurately known, a difficult requirement to meet. A more common practice is to compare the size structure of the catch made on different sizes of fishing gear to estimate the parameters of an assumed theoretical selection curve (e.g. Holt 1963), or to develop Type B selection curves (selection coefficient plotted against size of gear for a particular size class of fish).

In situations where the underlying form of the theoretical selection model is known or assumed (e.g. the logistic curve for trawl gear or the normal curve for gillnets), Type B curves have been used to estimate model parameters (see Hamley 1975 for a review of methods). In a more general context, however, comparative fishing studies provide little direct information about the shape or general form of an unknown selection curve (Pope et al. 1975). Still, comparative fishing can provide a basis for testing the validity of competing selection models.

If two different sizes of the same type of gear (e.g. hooks) are fished simultaneously on the same stock of fish with the same amount of fishing effort (i.e., $f_1 = f_2$ where the subscripts 1 and 2 refer to the smaller and larger gears, respectively), then as long as full vulnerability catchability is independent of gear size (i.e., $q_1 = q_2$), the ratio of catch in any common length class j ($C_{2,j}/C_{1,j}$) is equal to the ratio of selection coefficients

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

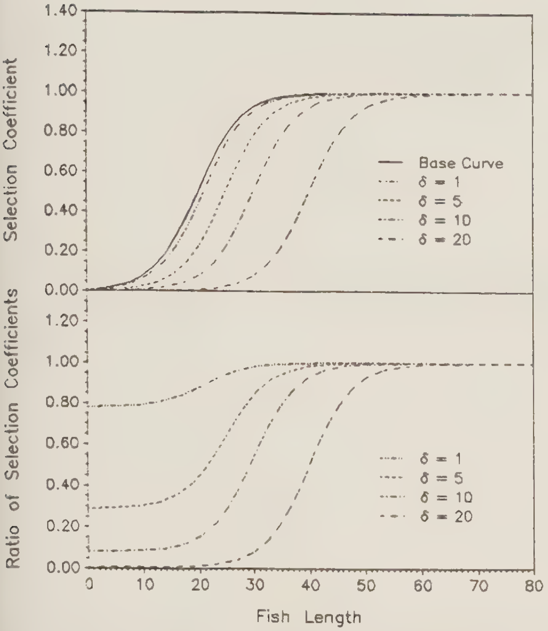

FIG. 2. Predicted ratios of catch taken on different sizes of a hypothetical fishing gear governed by logistic selection. See text for further explanation.

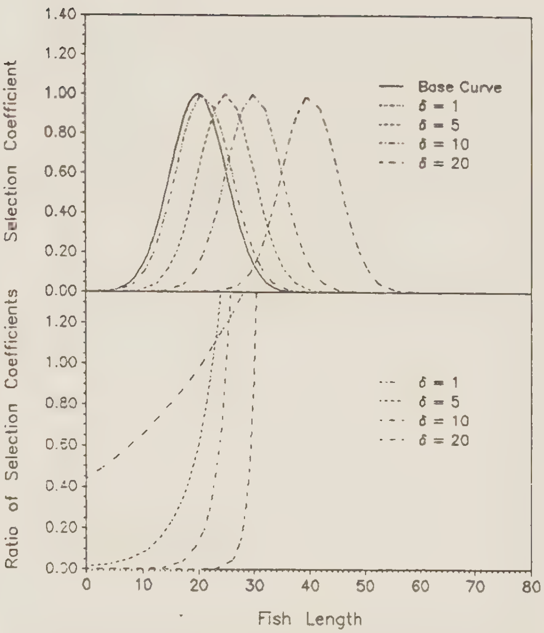

FIG. 3. Predicted ratios of catch taken on different sizes of a hypothetical fishing gear governed by normal selection. See text for further explanation.

$(s_{2,j}/s_{1,j})$. This property can be used to test the hypothesis that hook selectivity is best described by either the logistic or normal curves.

Specifically, if selection by fish hooks, like trawls, is governed by the logistic curve (Pope et al. 1975), then the ratio of catches taken on different hook sizes when plotted against length interval should, like the ratio of two logistic curves with common asymptote, increase asymptotically to a value of 1.00 (Fig. 2). Note that in the upper panel of the figure the standard base curve (solid line) depicts the selection curve for the smallest gear size. The other four curves represent selection curves for larger sizes of the same type of gear. Increasing gear size is presumed to simply shift selection curves to the right, without altering the asymptote or rate (i.e., steepness) parameters. The degree of shift is measured by δ, i.e., the difference between the scaling/position parameters of the selection curve for the larger gear and the base curve. The lower panel depicts the ratio of selection coefficients as a function of length, for each of the shifted curves relative to the base curve. This ratio consistently approachs a value of one.

Alternatively, if selection by hooks is, like gillnets, governed by the normal curve (Hamley 1975), then the ratio of catches by length interval should, like the ratio of two normal curves with similar height and dispersion parameters, increase geometrically without bound (Fig. 3). As in the preceding example, the upper panel depicts a base selection curve for the smallest gear size (solid line), with four selection curves from larger gears shifted progressively to the right. With increasing size of gear there is no alteration in the height or dispersion parameters of the selection curves. The degree of shift is again measured by δ, the difference in scaling parameters between each curve and the base. The ratio of selection coefficients, for each of the

TABLE 1. Catch of four deepwater snappers by fork length category and hook size.

Fork length (mm)	*Pristipomoides*						*Etelis carbunculus*	
	zonatus		*auricilla*		*flavipinnis*			
	#20	#28	#20	#28	#20	#28	#20	#28
200	2	1	0	0	0	0	0	0
220	3	2	1	0	0	0	2	0
240	9	5	2	0	0	0	1	2
260	27	23	21	5	0	0	5	4
280	46	48	36	11	0	0	16	13
300	92	84	97	30	2	2	30	41
320	138	169	142	44	7	4	35	41
340	181	226	157	50	15	11	69	95
360	236	334	169	62	25	19	80	76
380	280	405	115	41	51	51	63	83
400	228	379	50	24	54	44	25	56
420	175	255	3	2	20	34	12	19
440	61	88	0	0	15	24	7	17
460	2	9	0	0	7	6	2	7
480	0	1	1	0	0	3	2	2
500	0	1	0	0	1	1	0	1
520	0	0	0	0	0	0	0	0
540	0	0	0	0	0	0	1	0
Total	1480	2030	794	269	197	199	350	457
Species total	3510		1063		396		807	

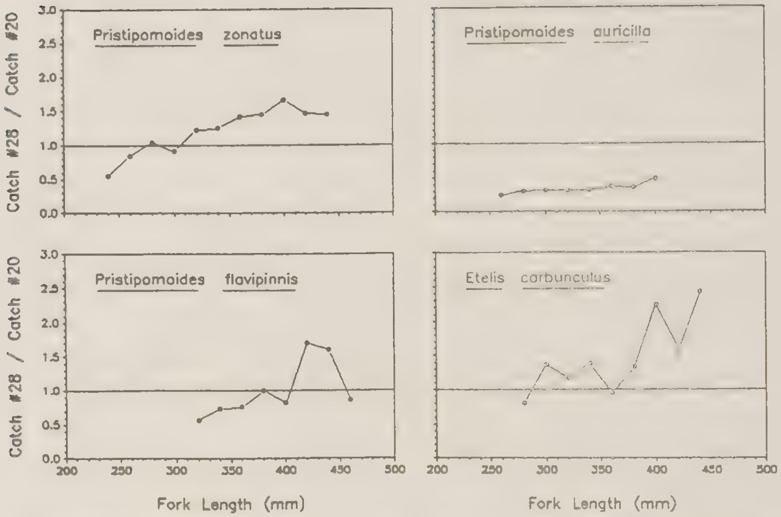

FIG. 4. Ratios of catches taken on #28 and #20 hooks, summarized by 20-mm FL categories, for the four species examined. A ratio of one corresponds to equal numbers of fish on the two hook sizes.

shifted curves relative to the base curve, is shown in the lower panel. In all cases the ratio of selection coefficients displays a precipitous monotonic increase.

Results

Over 7000 fish, comprising in excess of 30 species, were caught during handline fishing operations (see also Polovina 1986; Ralston and Williams 1988; Ralston 1988). However, 86% of the catch was composed of four snapper species: *Pristipomoides zonatus*, *P. auricilla*, *P. flavipinnis*, and *Etelis carbunculus*. Due to the relatively good catches of these four species, hook size catch ratios by length interval were calculated for each. Catch totals show (Table 1) that *P. zonatus* was particularly abundant, accounting for over half of all fish caught.

An examination of the size-specific ratio of catches taken on size #28 hooks, divided by the catches taken on size #20 hooks, shows a consistent increasing trend with FL for each species (Fig. 4). To reduce instability due to small sample size, catch ratios were calculated only if the combined sample size in a 20-mm interval of FL was ≥10.

Results for *P. zonatus* show that the smaller hooks caught more small fish than did the larger hooks (ratio <1.00). At a size of about 280 mm FL an equivalent number of fish were caught on each size of hook and at the larger sizes the largest hooks performed better. A Spearman rank correlation analysis of the *P. zonatus* data in Fig. 4 resulted in $r = 0.927$ ($P = 0.0001$), confirming the strong dependence between the size structure of the catch and the size of hook used.

Regardless of the size of fish, the smaller #20 hooks always caught more *P. auricilla* than did the larger #28 hooks, although to a lesser extent as fish size increased. Still, there was a strong Spearman rank correlation between fish size and the ratio of catch taken on the two hook sizes ($r = 0.976$, $P = 0.0001$). The low catch rate of *P. auricilla* on large hooks, in comparison to the other three snapper species, is likely due to its relatively small gape (Allen 1985) and planktivorous food habits (Seki and Callahan 1988).

For most sizes the catch of *P. flavipinnis* was generally greater on the small hooks than on the larger hooks, except in the largest length categories (FL >400 mm). Though not as strong as that of the preceding two species, a significant Spearman correlation existed between the size of *P. flavipinnis* and the ratio of catches taken on the size #28 and #20 hooks ($r = 0.786$, $P = 0.021$).

In contrast to the preceding two species, more *E. carbunculus* were caught on the #28 hooks than on the #20 hooks, especially in the largest size classes. As with all species examined, there was a significant Spearman rank correlation between fish size and catch ratio ($r = 0.767$, $P = 0.016$).

Discussion

The results presented here do not directly support either of the selectivity models presented earlier. The simple logistic model (Fig. 2) is not supported because the ratio of catches taken on the different hook sizes consistently rises to values in excess of 1.00. Likewise, the simple normal model (Fig. 3) is not supported because hook catch ratios do not seem to increase geometrically without bound.

Both these models are simple because full selection catchability is assumed to be unaffected by alterations in gear size (i.e., $q_1 = q_2$). There is evidence to show, however, that the catchability of optimally sized walleye to gillnets increases with increasing mesh size (Hamley and Regier 1973; Hamley 1975). Similarly, Beverton and Holt (1957) present data from alternating haul experiments showing that large mesh trawls catch more plaice in shared fully vulnerable size categories than do small mesh trawls, suggesting an increased efficiency of large mesh gear.

These findings demonstrate that increasing gear size can lead not only to a righthand shift of the selection curve, but also to an increase in catchability. Thus, the assumption that catchability in the fully vulnerable size range is independent of gear size is too simplistic.

If catchability varies the catch ratio is no longer equal to the simple ratio of selection coefficients, but includes the ratio of catchability coefficients as an additional term; that is:

$$C_{2,j}/C_{1,j} = (s_{2,j}/s_{1,j})(q_2/q_1)$$

Extending this result to a hypothetical model of logistic hook selection would suggest that catch ratios can exceed a value of one if $q_1 < q_2$. Catch ratios would then asymptotically approach a value equal to the ratio of catchability coefficients, rather than approaching a value of 1.00. The results presented in Fig. 4 (especially *P. zonatus*) are consistant with this interpretation, but they are not conclusive.

Conversely, a hypothetical model of hook selection based on righthand shifted normal curves in conjunction with progressively increasing full selection catchability coefficients, would simply accentuate the geometric unbounded increase evident in Fig. 3. Although none of the results presented in Fig. 4 seem to conform to such a pattern, it could be that the size range of fish sampled was too small to detect the strong curvature predicted by the model. Such an explanation, however, seems unlikely.

Our present understanding of the intrinsic nature of hook selectivity is rudimentary at best. There is no generally accepted theoretical model of selection by fish hooks, as there are for trawls, gillnets, and other meshed gears. It is likely that in reality neither of the models examined is particularly well-suited to the quantitative description of hook selectivity, although of the two, the logistic model is most consistent with the comparative fishing results presented here (see also Ralston 1982). What is needed is a direct determination (Pope et al. 1975) of selection coefficients through an experimental program, in which a population of known size structure is fished with hooks of various sizes. The sampled population could either be experimentally fished in captivity or it could be a known marked population in the field. The latter approach has been used effectively with gillnets (Hamley and Regier 1973) and was employed with limited success by Leclerc and Power (1980) in their work on angling and gillnet selectivities. In their study, however, small sample sizes prevented precise resolution of the selection pattern. Likewise, in two separate studies, Myhre (1969) compared the size structure of Pacific halibut captures with hooks against a known marked population, but he obtained conflicting results. Regardless, until a more definitive study is completed, it will be difficult to make inferences about the size structure of fish populations from single catch samples acquired with hook-and-line gear.

Acknowledgments

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References

ALLEN, G. R. 1985. FAO species catalogue. Snappers of the world. An annotated and illustrated catalogue of lutjanid fishes known to date. FAO Fish. Synop. (125), Vol. 6: 1–208.

BERTRAND, J. 1988. Selectivity of hooks in the handline fishery of the Saya de Malha Banks (Indian Ocean). Fish. Res. 6: 249–255.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (Gt. Brit.) Ser. II, 19: 533 p.

BROCK, V. E. 1962. On the nature of the selective fishing action of longline gear. Pac. Sci. 16: 3–14.

CLARK, J. R. 1960. Report on selectivity of fishing gear. *In* Fishing effort, the effect of fishing on resources and the selectivity of fishing gear. ICNAF Spec. Publ. 2: 27–36.

FORSTER, G. R. 1973. Line fishing on the continental slope: the selective effect of different hook patterns. J. Mar. Biol. Assoc. U.K. 53: 749–751.

1984. The distribution of fishes on the outer reef slopes of Aldabra (Indian Ocean) in relation to bottom temperatures. Environ. Biol. Fish. 10(3): 129–136.

HAMLEY, J. M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. 32: 1943–1969.

HAMLEY, J. M., AND H. A. REGIER. 1973. Direct estimates of gillnet selectivity to walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 817–830.

HOLT, S. J. 1963. A method for determining gear selectivity and its application. ICNAF Spec. Publ. 5: 106–115.

KANDA, K., A. KOIKE, S. TAKEUCHI, AND M. OGURA. 1978. Selectivity of the hook for mackerel, *Scomber japonicus* Houttuyn, pole fishing. J. Tokyo Univ. Fish. 61: 109–114.

KOIKE, A., AND K. KANDA. 1978. Selectivity of the hook of pond smelt, *Hypomesus olidus*. J. Tokyo Univ. Fish. 64: 115–123.

KOIKE, A., S. TAKEUCHI, M. OGURA, K. KANDA, AND C. ARIHARA. 1968. Selection curve of the hook of long line. J. Tokyo Univ. Fish. 55: 77–82.

LECLERC, J., AND G. POWER. 1980. Selectivity of fly-fishing, spinning and gillnet for brook charr and ouananiche in a large northern Quebec river. Environ. Biol. Fish. 5: 181–184.

MARGETTS, A. R. 1969. Comparative and experimental fishing as methods for studying fish behaviour in the natural habitat. FAO Fish. Rep. No. 62, Vol. 2: 131–138.

MCCRACKEN, F. D. 1963. Selection by codend meshes and hooks on cod, haddock, flatfish, and redfish, p. 131–155. *In* The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada.

MUNRO, J. L. 1983. Caribbean coral reef fishery resources. ICLARM Studies and Reviews 7. Inter. Center for Living Aquat. Res. Management, Manila, Philippines. 276 p.

MYHRE, R. J. 1969. Gear selection and Pacific halibut. Rep. Inter. Pacific Halibut Comm., No. 51: 33 p.

MYHRE, R. J., AND T. J. QUINN, II. 1984. Comparison of efficiency of snap gear to fixed-hook setline gear for catching Pacific halibut. Int. Pac. Halibut Comm., Sci. Rep. No. 69: 37 p.

POLOVINA, J. J. 1986. Variation in catch rates and species composition in handline catches of deepwater snappers and groupers in the Mariana Archipelago, p. 515–520. Proc. 5th Int. Coral Reef Congr. 1985, Tahiti.

POLOVINA, J. J., AND S. RALSTON. 1986. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. U.S. Fish. Bull. 84: 759–770.

POPE, J. A., A. R. MARGETTS, J. M. HAMLEY, AND E. F. AKYUZ. 1975. Manual of methods for fish stock assessment. Part III. Selectivity of fishing gear. FAO Fish. Tech. Pap. No. 41 (Rev. 1): 46 p.

RALSTON, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. Can. J. Fish. Aquat. Sci. 39: 1297–1302.

1988. Length–weight regressions and condition indices of lutjanids and other deep slope fishes from the Mariana Archipelago. Micronesica 21: 189–197.

RALSTON, S., R. M. GOODING, AND G. M. LUDWIG. 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. U.S. Fish. Bull. 84: 141–155.

RALSTON, S., AND H. A. WILLIAMS. 1988. Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-113, 47 p.

REGIER, H. A., AND D. S. ROBSON. 1966. Selectivity of gill nets, especially to lake whitefish. J. Fish. Res. Board Can. 23: 423–454.

ROLLEFSEN, G. 1953. The selectivity of different fishing gear used in Lofoten. J. Conseil 19: 191–194.

SAETERSDAL, G. 1963. Selectivity of long lines, p. 189–192. *In* The selectivity of fishing gear. Spec. Publ. No. 5. Int. Comm. Northwest Atl. Fish., Dartmouth, N.S., Canada.

SEKI, M. P., AND M. W. CALLAHAN. 1988. The feeding habits of two deep slope snappers, *Pristipomoides zonatus* and *P. auricilla*, at Pathfinder Reef, Mariana archipelago. U.S. Fish. Bull. 86: 807–811.

TAKEUCHI, S., AND A. KOIKE. 1969. The effect of size and shape of hook on the catching efficiency and selection curve of long-line. J. Tokyo Univ. Fish. 55: 119–124.

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Gonad Morphology, Histology, and Spermatogenesis in South Pacific Albacore Tuna *Thunnus alalunga* (Scombridae)

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The reproductive biology of tuna, and the albacore *Thunnus alalunga* in particular, is not well understood with respect to functional morphology of the gonads in relation to sexual maturity. In the course of an investigation of the genetic variability of albacore, differences in morphology were observed between the right and left gonad of male and female fish and the size of the fat body associated with the gonads. Histological examinations were made to determine the relationship between these morphological differences and the reproductive state of the gonads. In this paper we report findings made on gonad morphology, histology, and spermatogenesis and relate them to the reproductive biology of this species.

Materials and methods

Albacore specimens were collected onboard the U.S. NOAA RV *Townsend Cromwell* and the New Zealand RV *Kaharoa* during cooperative studies conducted in 1986 and 1987 to investigate the biology/ecology and fishery exploration of albacore tuna in the South Pacific Ocean (Laurs 1986, Laurs et al. 1987). The fish were caught using standard albacore troll-fishing methods (Dotson 1980). In addition, specimens were collected during commercial fishing operations conducted in 1987 by Japanese longline vessels. Locations of specimen collection are summarized in Table 1.

Soon after the fish were caught, fork lengths were measured to the nearest millimeter and the gonads and associated fat body were dissected from each fish. The right and left gonads were preserved separately in 10% neutral buffered formalin. Histological preparations were initiated by washing the tissue in running water for 12 hours. An American Optical T/P tissue processor was used to dehydrate and embed the tissue in paraplast. The tissue was sectioned at 5 microns and stained with Harris' hematoxylin followed by eosin counter stain (Humason 1979, Gabe 1976).

Each testis subsample histological preparation was classified according to (a) estimates of the relative abundances of spermatocytes, spermatids, and sperm; (b) sperm-duct development; and (c) sexual maturity. In addition, the cross-sectional area of the medial section of each testis was determined. Electron micrographs were prepared of sperm, which had been washed from the sperm duct of selected testes with physiological saline and fixed in 3% gluteraldehyde in 0.1 M phosphate buffer.

Results

We observed asymmetrical differences in the size of both ovaries and testes and in the size of the fat body associated with gonads from both sexes of fish. Histological examination showed that all stages of sexual maturity were represented in the specimens of testes, allowing us to describe spermatogenesis. No sexually mature ovaries were found, limiting the results for females to asymmetrical size differences.

Number and size of fish examined

Gonads from 197 albacore were examined histologically during the study. Sex ratio was nearly 1:1, with 106 males and 91 females. The fish ranged in fork length (FL) from 50 to 101 cm. Over 90% of females and over 80% of males were less than 90 cm FL, the size at which sexual maturity is believed to first occur in female albacore (Ueyanagi 1955, Otsu and Uchida 1959, Otsu and Hansen 1961). Length-frequency distributions of the fish examined are given in Figure 1.

Gonad general morphology

As in most teleosts, the gonads in male and female albacore are paired, elongate organs, located in the dorsal portion of the body cavity. They

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Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1

Summary of information on *Thunnus alalunga* specimens used in study.

Ship	Date	No. species	Fork length (cm) Range	Fork length (cm) Median	Location in South Pacific
RV *Townsend Cromwell*	1986 17–21 Feb.	33	50.6–84.4	71.5	Central lat. 38°–40°S long. 146°–152°W
RV *Townsend Cromwell*	1987 25 Jan–1 Feb.	33	50.6–97.5	63.8	Central lat. 35°–39°S long. 151°–157°W
RV *Kaharoa*	1986 15 Feb.–28 Mar.	13	50.0–76.0	70.0	Western lat. 33°–44°S long. 166°E–178°W
FV *Wakashio*	1987 21 June	9	63.0–98.0	88.0	Western lat. 37°S long. 179°E
FV *Zuiho*	1987 20–23 June	18	85.2–101.1	94.5	Western lat. 37°–38°S long. 179°E

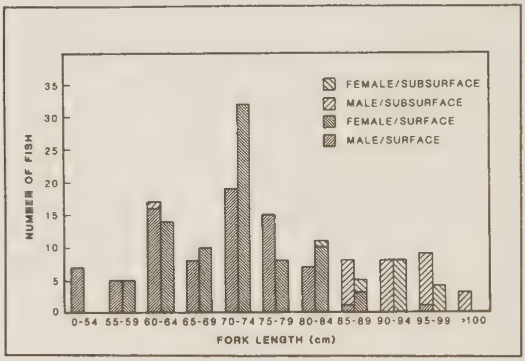

Figure 1

Length-frequency distributions for male and female South Pacific albacore tuna examined in this study. Surface troll-caught fish and subsurface longline-caught fish are differentiated.

are suspended by the mesentery which contains a fat body closely associated with the gonad between it and the dorsal body wall (Godsil and Byers 1944). The fat body will be discussed in a later section. Testes are thin and ribbon-like in immature fish, and develop into somewhat flattened, whitish-yellow organs which are relatively solid as the fish advance in maturity. Ovaries in immature fish closely resemble immature testes in appearance. They become progressively enlarged in length and girth and tend to be somewhat pinkish in color as the fish progresses in maturity.

We initially made casual observations, when collecting gonad tissue samples for genetic-variability studies of North Pacific albacore, that the right gonads were most often larger than those on the left side. The present study of nearly 200 South Pacific albacore showed that while right and left gonads of both sexes were about the same length, the cross-sectional area and volume of the right ovaries and testes were regularly larger than those on the left side. Figure 2 shows a pair of ovaries and associated fat bodies, portion of the digestive tract, and ventral fin dissected from a 94-cm FL North Pacific albacore. The disparity in size between the right and left ovaries and associated fatty bodies is typical of what we have observed in this study and in casual observations.

Size differences between right and left testes

Measurements of the cross-sectional area (mm^2) of the medial sections of the right and left testes provide quantitative estimates of size differences between the two. Data summarized in Table 2 show that the right testis was larger than the left in 72% of male fish examined, the two testes were equal in size in 2%, and the left was larger than the right in 23%.

The results given in Figure 3 show that the dissimilarity in size increases with increasing fork length. The right testis is about 28–32% larger than the left in fish less than 80 cm FL, but increases to about 66–75% larger in fish over 80 cm. Data on displacement volumes measured on a sample of the right and left testes showed results similar to those made on the measurements of cross section. Examination of relationships between fork length and cross-sectional area of the

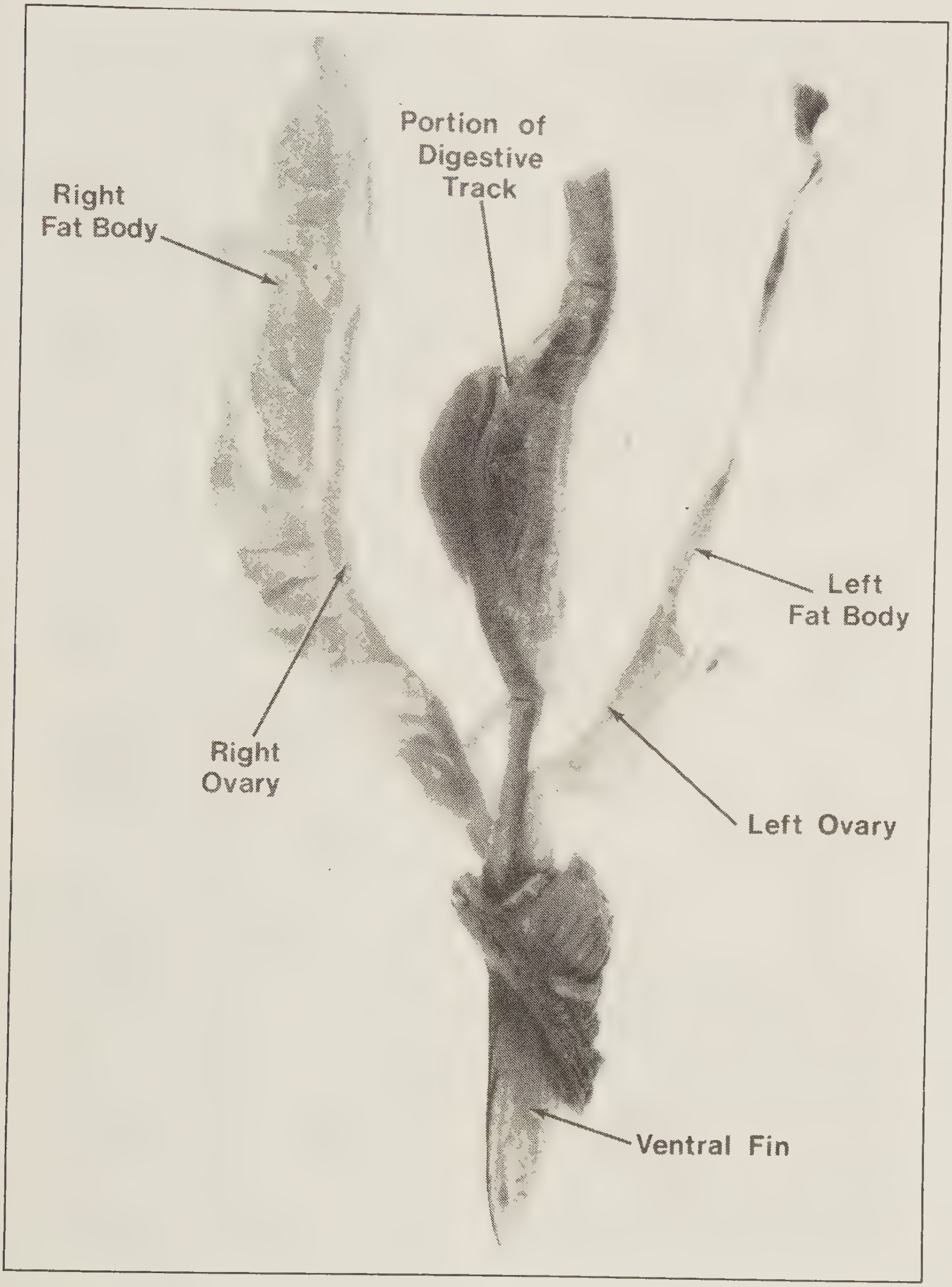
Portion of Digestive Track
Right Fat Body
Left Fat Body
Right Ovary
Left Ovary
Ventral Fin

Figure 2

Pair of ovaries and associated fat bodies, portion of digestive system, and ventral fin from a 94-cm FL albacore tuna caught in the North Pacific.

Table 2
Relative size of right and left testes, *Thunnus alalunga* ($n = 106$).

Relative size of testes	Percent occurrence
Right larger than left	72
Right equal to left	2
Right smaller than left	23
No data	3

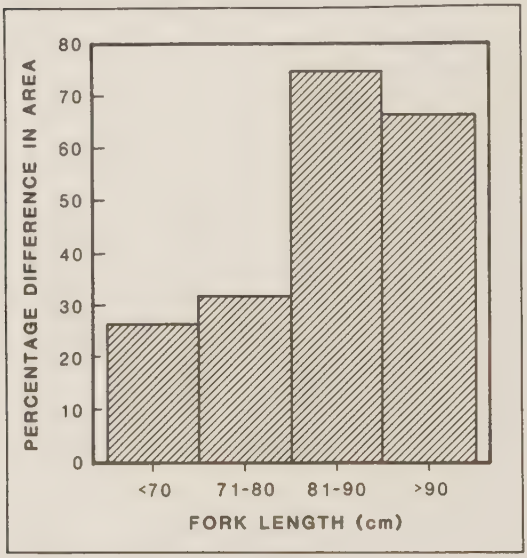

Figure 3
Percentage difference in cross-sectional area of the medial sections of right and left testes of South Pacific albacore, by fork-length.

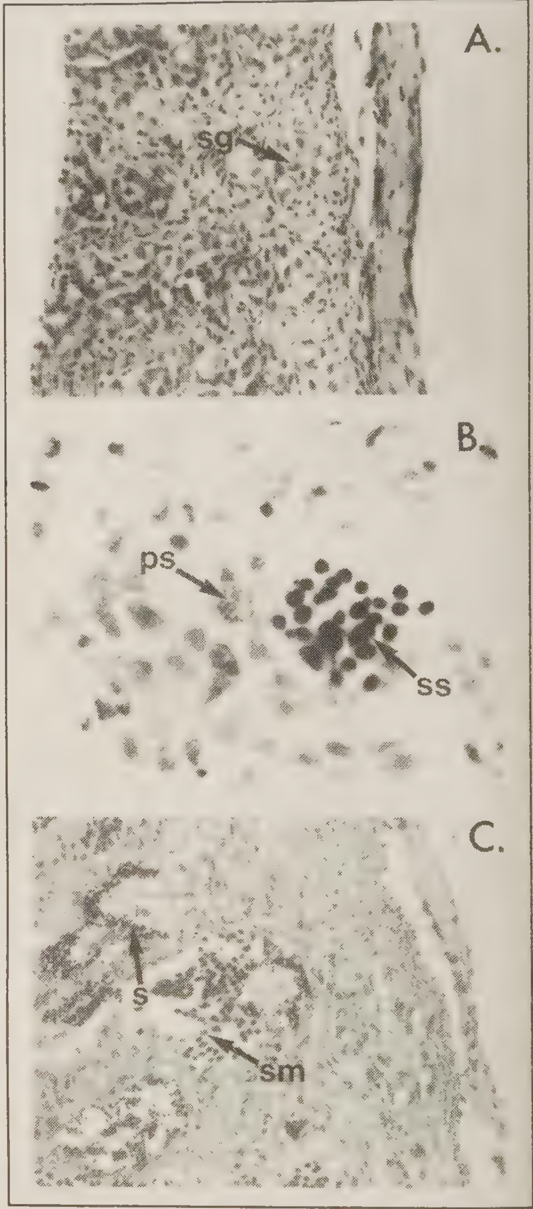

Figure 4
Spermatogenic cells observed in testes of South Pacific albacore. (A) Spermatogonia (sg) situated on lobule wall (×400); (B) primary spermatocyte (ps) cells and secondary spermatocyte (ss) cells (×600); (C) spermatids (sm) and spermatozoa (s) (×400).

right and left testes showed that the sizes of both gonads increase exponentially with increasing length of the fish, and that the area of the right testis does not increase at a faster rate than the left.

In summary, the right testis is predominately larger than the left; however, they both appear to increase in size at similar rates as the fish increases in length.

Histology of testes

The albacore testis has a lobular-type cellular arrangement, characteristic of most teleosts (Billard et al. 1982). We classified the germ cells into the following phases of development: spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and spermatozoa.

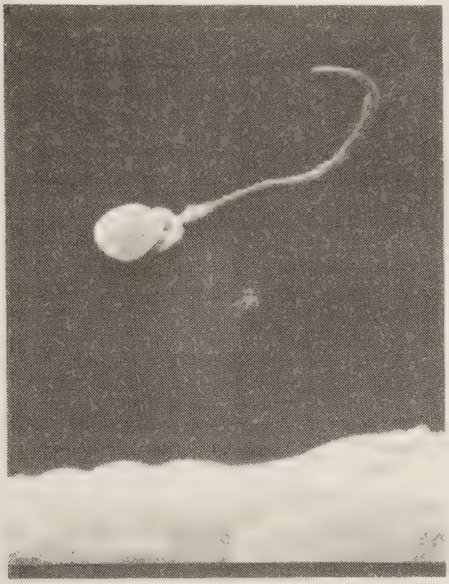

Figure 5
Electron micrograph of South Pacific albacore spermatozoa (scale indicates 1 μm).

The primary spermatogonia are the largest cells with diameters of 12–16 μm. They have a prominent nucleolus, are basophilic, and are found in cysts with varying numbers of individual cells. The cysts are usually found singly near the periphery of the testis; a cyst situated on the lobule wall is shown in Figure 4A.

Primary spermatocytes are oval or spherical with diameters of 8–12 μm. They have no visible nuclear membrane and the chromatin material occupies most of the cell. Figure 4B shows examples of primary spermatocytes. Secondary spermatocytes are very small, spherical cells with diameters of 4–7 μm. Unlike primary spermatocytes, the chromatin is found in a clumped condition, similar to the spermatids. The cells occur in groups and are strongly basophilic. Figure 4B shows secondary spermatocytes.

Spermatids are strongly basophilic spherical cells with diameters of 2–4 μm. As they mature, they become smaller and the chromatin becomes uniformly condensed. Figure 4C shows that after detaching from the lobule wall, the spermatids remain in dense clusters.

The spermatozoa have a rounded nucleus and are morphologically subdivided into head, neck piece, short midpiece, and tail; as in other teleosts, there is no acrosome. They measure 1–2 μm in diameter, excluding the tail. An electron micrograph of an individual sperm is shown in Figure 5.

Table 3
Differences in meiotic activity between right and left testes, *Thunnus alalunga* ($n = 106$).

Meiotic activity	Percent occurrence
Left < right	10
Left = right	26
Left > right	61
No data	3

Meiotic activity

Relative abundances of sperm, spermatids, and spermatocytes were taken as a measure of meiotic activity. As previously discussed, the albacore testes were generally asymmetrical in size with the right testis more often larger than the left. However, we found that meiotic activity and sperm-duct development showed the opposite relationship. The left testis was meiotically more active than the right in 61% of males examined, the left and right testes had about equal activity in 26%, and the right was more active than the left in 10% (see Table 3).

Examination of data for each pair of testes showed a 60% occurrence of greater meiotic activity in the left testis relative to larger size of the right testis. Other combinations of meiotic activity and relative size of testes showed a 15% or less occurrence (see Fig. 6).

Relative abundance of sperm, spermatids, and spermatocytes

Absolute counts of the number of spermatogenic cells would be exceedingly difficult to make. Instead we estimated relative abundances of spermatocytes, spermatids, and sperm present using the categories *none*, *few*, *some*, and *many*. The results show that for all sizes of fish, the relative abundance of sperm was higher in the left testis than the right testis. For example, there were nearly 2 times more *many* and 2½ times fewer *none* categories of sperm observed for the left than the right testis. In both the left and right testes of fish in all sizes, relative abundance of sperm was highest in the caudal portion and decreased towards the rostral end (Figure 7).

The findings are similar for spermatids and spermatocytes, but the differences between testes are not as pronounced as those for sperm. For all sizes of fish, relative abundances of both spermatids and spermatocytes were higher in the left than the right testis. For the left testis, there were about 20% and 30% more *many* and 40% and 50% fewer *none*, categories observed for spermatids and spermatocytes, respectively,

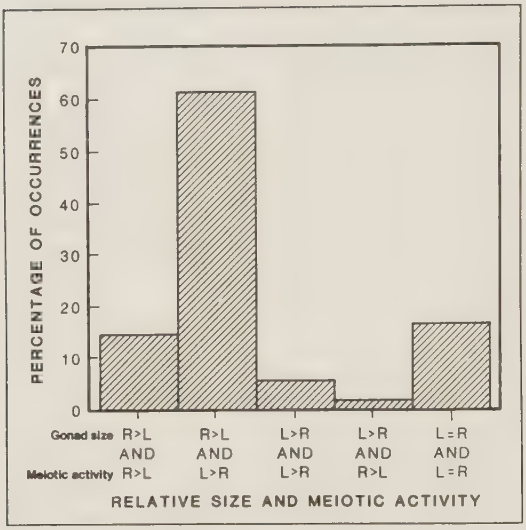

Figure 6
Percentage occurrence of relative level of meiotic activity and relative size of right (R) and left (L) gonads of South Pacific albacore. On the abscissa, upper expression refers to relative gonad size, and lower expression refers to relative level of meiotic activity.

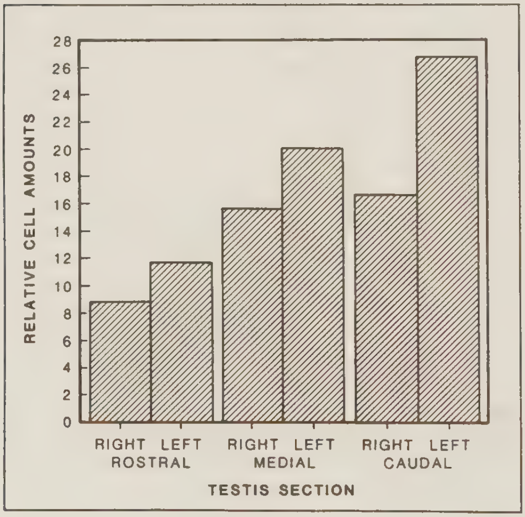

Figure 7
Relative abundance of sperm in rostral, medial, and caudal portions of the right and left testes of South Pacific albacore.

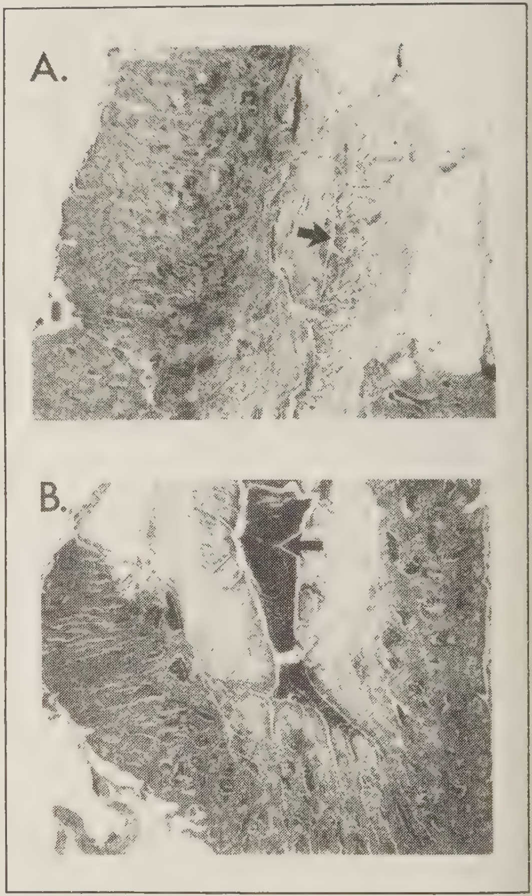

Figure 8
(A) Empty sperm duct of an immature South Pacific albacore; (B) sperm duct of a mature albacore filled with sperm, ×100.

than for the right testis. The relative abundance of each group of germ cells was highest in the caudal portion and decreased towards the rostral portion in both the left and right testes in all sizes of fish.

Sperm duct development

During testicular morphogenesis, teleost sperm ducts are formed by somatic cells derived from the somatic wall (Nagahama 1983). The main duct is present in immature albacore testes (Fig. 8A) in which no sperm are found. In mature albacore, we observed that the sperm duct is located near the center of the testis (Fig. 8B) and that a branching system of tubules radiates toward and end blindly at the testicular periphery. These obser-

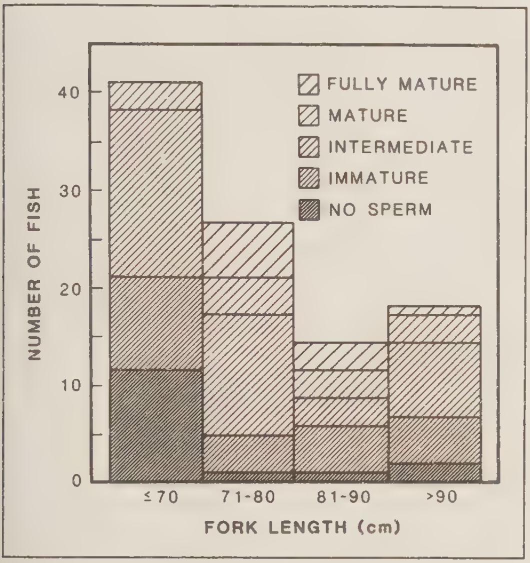

Figure 9
Comparison of sexual maturity levels of male South Pacific albacore by fork length.

Table 4
Percentage sexual maturity of fish by fork length.

Stage of sexual maturity	Fork length (cm)			
	<70	71–80	81–90	>90
No sperm present and immature	51	18	40	37
Intermediate	42	46	20	42
Mature and fully mature	7	36	40	21

vations differ from those reported for many other teleosts, where the main duct is located along the dorsal surface of the testis and may not be present in immature stages of the testis (Grier et al. 1980).

As the production of sperm increases, morphological changes occur in the main sperm duct. In the immature testis the main sperm duct is thin-walled and highly convoluted (Fig. 8A). In the mature testis the main duct, when filled with sperm, has much thicker walls and is less convoluted and more rounded (Fig. 8B). The production of sperm is also associated with increased vascularization of the testis, first in the caudal portion followed by the medial and rostral portions.

Ratios of observations characterizing immature and mature stages of sperm-duct development (thin:thick, convoluted:round, large:small) showed a higher proportion of mature sperm ducts in the left testis than the right. The results also reveal that sperm-duct development is greatest in the caudal, intermediate in the medial, and least in the rostral portions of both the right and left testes. As expected, there was an increasing trend in sperm-duct development with increasing fork length.

Sexual maturity

Fish were classified into five levels of sexual maturity based on relative abundance of sperm observed in the testes: (1) No sperm present in any portion of either testis; (2) immature, few sperm observed in one or more portions of either or both testes; (3) intermediate, few or some sperm in more than one portion of both testes, but not the sperm duct; (4) mature, many sperm observed in most portions of both testes and the sperm duct; and (5) fully mature, many sperm observed in all portions of both testes and the sperm duct.

Information on sexual maturity in relation to fork-length size categories is given in Figure 9 and Table 4. Slightly more than 50% of fish 50–70 cm FL were immature, including 28% (derived from Figure 9) with no sperm present in any portion of either testis. Over 40% were in the intermediate level and 7% were judged sexually mature, but none was fully mature. Fish in size groups larger than 70 cm FL had a lower proportion of immature individuals than did fish less than 70 cm, ranging from 18% to 40% (Table 4), including only 3–10% with no sperm present in any portion of either testis (derived from Figure 9). The proportion of fish in the intermediate level of maturity ranged between 20% and 46% for fish in size groups larger than 70 cm FL. The percentages of fish in the mature and fully mature categories were nearly the same for size groups 71–80 cm and 81–90 cm FL, 36% and 40%, respectively, but only 21% for the size group over 90 cm. The 71–80 cm FL size group had the highest proportion of fully sexually mature individuals, 23%, while only about 5% of fish larger than 90 cm were fully sexually mature (derived from Figure 9).

The lower proportion of mature and fully mature individuals in the size group larger than 90 cm FL appears to be related to geographic region and/or type of fishing gear. Figure 10 compares maturity levels between fish caught in the midocean region of the central South Pacific by surface trolling and those caught in coastal waters off New Zealand by subsurface longline. It is evident in Figure 10 that a higher proportion of immature and a lower proportion of mature and fully mature individuals were caught in coastal waters than in the midocean region, even though the longline-caught fish were much larger, averaging 92.3

cm FL, than troll-caught fish, averaging 69.2 cm. Figure 1 shows that virtually all of the fish in the size category greater than 90 cm were caught in coastal waters by subsurface longline.

Fat body

A lobulated mass of fat-like tissue was usually observed in the mesentery attached to testes and ovaries. In some cases it was extremely large and well developed, but quite rudimentary in others. It was generally white-to-creamy in color and always formed in segmental lobes. The extent of the fat body was usually coincident with that of the gonad, but sometimes it extended a variable distance anteriorly beyond the gonad. The mass of the fat body was generally correlated with size of the gonad. We observed that the right testis or ovary of the albacore, which is generally larger than the left, usually had a larger fat body (see Figure 2). In addition, we observed that the fat body was proportionately larger in immature fish that were meiotically inactive than in fish with gonads actively producing sperm.

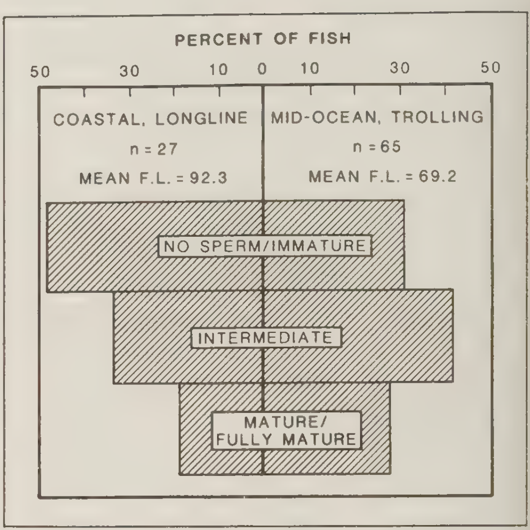

Figure 10
Comparison of sexual maturity levels of male albacore caught in coastal South Pacific waters by subsurface longline (left) with those caught in midocean South Pacific region by surface trolling (right).

Discussion

According to literature pertaining to the general structure and function of teleost gonads, the development of gonads is usually similar on both sides of the fish. However, asymmetry in gonad size has been observed sometimes in some species, usually at or near the time of breeding (Turner 1919, Robertson 1957, Sanwal and Khana 1972, Dalela et al. 1977).

Asymmetry in gonad size appears to be common for albacore, at least in prespawning stages. We observed asymmetry in 95% of fish examined, with the right gonad larger than the left in 72% of the cases. The disparity in size increased with increasing fork length. The right testis averaged about 30% larger than the left in fish less than 80 cm and averaged more than 70% larger in fish greater than 80 cm. We do not have data collected during active spawning to ascertain if this relationship exists at that stage.

Otsu and Uchida (1959) reported that the right ovary was usually slightly larger than the left in albacore specimens from the central North Pacific, but they did not quantify the difference. Ueyanagi (1955) noted that the right and left ovaries from a mature female albacore caught in the Indian Ocean differed in weight by 100 grams. However, he did not indicate weights or relative size of the ovaries. Partlo (1955) conducted histological studies on 44 albacore from the eastern North Pacific, but did not publish data on gonad size or mention asymmetry. The gonads of other tunas are more or less symmetrical in size and usually have no conspicuous fat body (Kurt Schaefer, Inter-Am. Trop. Tuna Comm., P.O. Box 271, La Jolla, CA 92038, pers. comm., 1 May 1989).

The finding that meiotic activity is higher in the smaller of a pair of testes is puzzling, and we have no ready explanation for it. It may be that this relationship holds true only for prespawning individuals and possibly during other periods when albacore are not spawning. We are unable to determine whether this condition continues through the spawning cycle because our samples were collected over an insufficient period and not in the primary geographic region where South Pacific albacore are believed to spawn (Otsu and Hansen 1961). A remote possibility is that the smaller testis is kept in an advanced reproductive state for "opportunistic" spawning and that the larger testis matures only when the fish is in the more prevalent location of spawning. If this is so, the species could presumably extend its reproductive potential with relatively low expenditures of energy. It is also possible that sperm are not shed by precocious fish, but are reabsorbed. Progressive reabsorption of sperm by sertoli cells has been observed in rainbow trout (van den Hurk et al. 1978).

Our results show that some males less than 70 cm may be sexually mature and that the proportion of sexually mature individuals increases with increasing fork length, up to 90 cm. There is a decrease in the percentage of sexually mature males in the size category above 90 cm FL which may be related to the method of capture and/or the type of habitat where collected. All fish larger than 90 cm, except one, were caught during subsurface longline fishing operations within about 75 miles of the coast of the New Zealand north island, whereas nearly all other fish were caught by surface trolling in midocean waters. Oceanographic observations made concurrently with albacore troll-fishing operations indicate that albacore in the midocean region of the South Pacific are associated with Subtropical Convergence Waters (Laurs 1986, Laurs et al. 1987).

Female albacore have been reported to attain sexual maturity and first spawn at about 90 cm FL (Ueyanagi 1955, Otsu and Uchida 1959); however, size at maturity for males has not been well established. Otsu and Hansen (1961) found that some male albacore are probably mature when they attain a length of about 90 cm FL. Based on the general appearance of testes and oozing of milt, Ueyanagi (1957) postulated the smallest mature male to be 97 cm FL in a sample of albacore collected in the western North Pacific. Brock (1943) reported that "Milt could be squeezed from the testes of some of the more mature males, but no females were found in which eggs could be discerned by the unaided eye. . . ." Brock (1943) examined fish caught off the Oregon coast that ranged in fork length between 53 and 90 cm, but did not specify the size of fish that contained milt.

Partlo (1955), in the only published histological study that includes albacore testes as well as ovaries, concluded that both males and females in his age groups V and VI were in a condition approaching spawning. He calculated that the mean fork length for males and females in age-group V is approximately 70 cm, and for age-group VI is about 85 cm for males and 79 cm for females. He also reported observing small numbers of fully mature sperm restricted to tubules of the posterior portion of testes in age-group IV, which he reported as having a mean fork length of 62 cm. Partlo (1955) examined a total of 44 testes and ovaries, but unfortunately did not specify the sex or number of individuals in each age group.

Godsil and Byers (1944) reported that the fat body was present in albacore collected throughout the North Pacific, except in three specimens from the area around the Hawaiian Islands, with its greatest development always on the right side of the fish. However, they made no mention of asymmetry in gonad size.

There appears to be a functional relationship between meiotic activity and the amount of fat in the mesentery. We presume the fat body provides an energy source for spermatogenesis, although we have no information from the present study on the timing of sperm release from the albacore testis. Godsil and Byers (1944) also speculated that the fat body acts as an energy reserve for female albacore that is expended during the spawning season. They based their supposition on the absence of the fat body in three recently spawned albacore from the Hawaiian Islands. Schaefer (1987) noted that spawning in the black skipjack, *Euthynnus lineatus*, is probably regulated by energy available in fat storage. When the fat stores fall below a minimum level, ovarian atresia probably occurs over a short period of time.

Conclusions

We provide quantitative evidence that a substantial portion of male albacore caught in midocean areas of the South Pacific Subtropical Convergence Zone about lat. 35°–40°S, may be sexually mature when they attain a fork length of 71–80 cm. Also, the proportion of mature fish increases with increasing length. A lower proportion of males caught by subsurface longline fishing in coastal waters off New Zealand showed development in sexual maturity, although not as accelerated as males caught by surface trolling in the midocean region. Female fish 55–95 cm FL caught in both regions showed few signs of sexual maturation. South Pacific albacore are believed to spawn generally in the region of the Southern Tropical Convergence waters about lat. 20°–10°S (Knox 1970). This region is about 1000–1500 miles north of the Subtropical Convergence Zone where the albacore investigated in this study were caught.

The adaptive significance of sexual maturity in male albacore at times, locations, and ages when females are not in spawning condition is not clear. Sampling of both males and females over the entire spawning cycle and in locations where albacore are believed to spawn will be required to understand the reproductive biology of the South Pacific albacore population.

Acknowledgments

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Citations

Billard, R., A. Fostier, C. Weil, and B. Breton

1982 Endocrine control of spermatogenesis in teleost fish. Can. J. Fish. Aquat. Sci. 39:65–79.

Brock, V.E.

1943 Contribution to the biology of the albacore (*Germ alalunga*) of the Oregon coast and other parts of the North Pacific. Stanford Ichthyol. Bull. (2)6:199–248.

Dalela, R.C., M. Rana, and S.R. Verma

1977 Season histological changes in the gonads of two teleost fishes, *Notopterus notopterus* (Pallus) and *Colisa fasciatus*. Gegenbaurs Morphol. Jahrb. 132:128–140.

Dotson, R.C.

1980 Fishing methods and equipment of the U.S. west coast albacore fleet. NOAA Tech. Memo TM-NMFS-SWFC-8, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, Ca 92038, 126 p.

Gabe, M.

1976 Histological techniques [Transl. R.E. Blacheith]. Springer-Verlag, NY, 1106 p.

Godsil, H.C., and R.D. Byers

1944 A systematic study of the Pacific tunas. Calif. Dep. Fish Game Fish. Bull. 50, 131 p.

Grier, H.J., J.R. Linton, J.F. Leatherland, and V.L. de Vlaming

1980 Structural evidence for two different testicular types in teleost fishes. Am. J. Anat. 159:331–345.

Humason, G.L.

1979 Animal tissue techniques. W.H. Freeman, San Francisco, 661 p.

Knox, G.A.

1970 Biological oceanography of the South Pacific. *In* Wooster, W.S. (ed.), Scientific exploration of the South Pacific, p. 155–182. Natl. Acad. Sci., Wash., DC.

Laurs, R.M.

1986 U.S. albacore trolling exploration conducted in the South Pacific during February–March, 1986. NOAA Tech. Memo. TM-NMFS-SWFC-66, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 30 p.

Laurs, R.M., K. Bliss, J. Weatherall, and B. Nishimoto

1987 South Pacific albacore fishery exploration conducted by U.S. jig boats during early 1987. Admin. Rep. LJ-87-22, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA 92038, 31 p. + append. 21 p.

Nagahama, Y.

1983 The functional morphology of teleost gonads. *In* Hoar, W.S., et al. (eds.), Fish physiology, Vol. IX A, p. 223–274. Acad. Press, NY.

Otsu, T., and R.J. Hansen

1961 Sexual maturity and spawning of the albacore in the Central South Pacific Ocean. Manuscr. to Pacific Tuna Biology Conf., Honolulu, Aug. 1961. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, 26 p.

Otsu, T., and R. Uchida

1959 Sexual maturity and spawning of albacore in the Pacific Ocean. U.S. Fish Wildl. Serv. Fish. Bull. 148:287–305.

Partlo, J.M.

1955 Histological studies on albacore (*Thunnus alalunga*) gonads from the eastern Pacific. J. Fish. Res. Board Can. 12(1):61–67.

Robertson, D.H.

1957 Accelerated development of testes after unilateral gonadectomy, with observations of the normal testes of rainbow trout. U.S. Fish Wildl. Serv. Fish. Bull. 127:9–30.

Sanwal, R., and S.S. Khanna

1972 Seasonal changes in the testes of a freshwater fish *Channa gachua*. Acta Anat. 83:139–148.

Schaefer, K.M.

1987 Reproductive biology of black skipjack, *Euthynnus lineatus*, an eastern Pacific tuna. Inter-Am. Trop. Tuna Comm. Bull. 19(2):164–260.

Turner, C.L.

1919 The seasonal cycle of spermary of the perch. J. Morphol. 32:681–711.

Ueyanagi, S.

1955 On the ripe ovary of the albacore, *Germo germo* (Lacepede), taken from the Indian Ocean. Bull. Jpn. Soc. Sci. Fish. 20(12):1050–1053.

1957 Spawning of the albacore in the Western Pacific. Rep. Nankai Reg. Fish. Res. Lab. 6:113–124.

van den Hurk, R., J.A. Vermeij, J. Stegenga, J. Peute, and P.G.W.J. van Oordt

1978 Cyclic changes in the testis and vas deferens of the rainbow trout (*Salmo gairdneri*) with special reference to sites of steroidogenesis. Ann. Biol. Anim. Biochim. Biophys. 18: 899–904.

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Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific

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ABSTRACT: Large-scale patterns of dolphin distribution and oceanography were studied from research-vessel surveys conducted in the pelagic eastern tropical Pacific during June to November 1982, 1986 and 1987. Substantial changes were observed in relation to previously reported winter distributions for spotted and/or spinner dolphin schools (*Stenella attenuata* and/or *S. longirostris*)and for striped dolphin schools (*S. coeruleoalba*). These dolphin species were sighted in abundance west of 120° W along 10° N coincident with seasonal shoaling of a thermocline ridge. No seasonal distribution changes were observed for common dolphin schools (*Delphinus delphis*); as in the winter, they occupied upwelling-modified waters of the region. Highest-density areas for the 3 school types were clearly separated spatially, and the thermocline depths and sigma-t's of sighting localities were statistically different between spotted/spinner dolphin schools and common dolphin schools. Striped dolphin schools could not be discriminated from the other 2 types based on these habitat variables, indicating other factors or processes contribute to the observed spatial separation of the 3 distributions.

INTRODUCTION

Unlike large whales, the smaller cetaceans are not known to undertake extensive seasonal migrations (Gaskin 1982). Among the delphinids, smaller-scale seasonal movements have been observed for some temperate, relatively coastal populations, apparently in response to seasonal movements of prey (Jonsgard & Lyshoel 1970, Mercer 1975, Condy et al. 1978, Leatherwood & Walker 1979, Selzer & Payne 1988) or seasonal habitat fluctuations (Tomilin 1967, Miyazaki et al. 1974, Viale 1985).

Seasonal distribution changes have not been clearly documented for dolphin populations in the tropics, where seasonal environmental changes are relatively small (Pickard & Emery 1982). Returns from 7 tagged spotted dolphins *Stenella attenuata* in the eastern tropical Pacific (ETP) suggest an E–W movement pattern, but these data are too few to be conclusive (Perrin et al. 1979). One objective of this study was to test for seasonal shifts in distributions of eastern tropical Pacific dolphins, and if observed, to examine possible relationships with seasonal environmental changes. A second, related objective was to quantify the associations of dolphin distributions with simple indices of physical habitat, and test for habitat differences among species.

Aggregations of pelagic dolphins, tunas and birds regularly forage together in the eastern tropical Pacific (Perrin 1969, Au & Perryman 1985). Four dolphin species are involved: spotted dolphins, spinner dolphins *Stenella longirostris*, striped dolphins *S. coeruleoalba* and common dolphins *Delphinus delphis*. However, most aggregations contain spotted and spinner dolphins, or just spotted dolphins. Common dolphins are infrequently found with both birds and tunas, and striped dolphins are only rarely involved. Dolphins are incidentally killed in the course of commercial purse seine tuna fishing in the ETP, raising concerns for their conservation (Smith 1983, Perrin 1988).

Historical distribution ranges of spotted, spinner, striped and common dolphins in the ETP (Figs. 1 and 2) have been defined from summaries of many thousands of sighting and collection localities (Evans 1975, Perrin 1975, Perrin et al. 1983, 1985). Au & Perryman (1985) investigated distribution patterns and habitat relationships within these ranges during the northern winter (January to March), from research-vessel sighting surveys. They reported 2 complementary patterns. In

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winter, spotted and spinner dolphins (Fig. 1) occurred primarily north of the equator extending offshore from the coast of Mexico and Central America, but also south of the Galapagos Islands. Common and striped dolphins occurred primarily along the equator, off Baja California, Costa Rica, and northern South America (Fig. 2). Au & Perryman (1985) hypothesized from these patterns that spotted and spinner habitat was characterized by warm, low-saline tropical waters where intermediate to shallow thermoclines and relatively small annual variations in surface conditions occurred. In contrast, they hypothesized common and striped dolphin habitat to be characterized by cooler, more saline 'upwelling-modified' waters. Major concentrations of dolphins along 10° N, between 120 and 150° W, were noticeably absent in the winter data (Figs. 1 and 2). These western concentrations are a dominant feature of the known historical distributions, suggesting that they are a seasonal feature, not present in the winter.

In this study geographic patterns of dolphin sightings made from research vessels during the northern summer were examined in comparison with winter sighting patterns reported by Au & Perryman (1985) for evidence of seasonal distribution changes. Their hypotheses were also tested about habitat characteristics and separation among dolphin school types.

STUDY AREA

Basic oceanographic patterns. The basic physical features of the upper ocean in the eastern tropical Pacific have been described by Wooster & Cromwell (1958), Wyrtki (1964, 1965a, b, 1966, 1967), and Tsuchiya (1970, 1974, 1982). The major surface water masses and currents are shown in Fig. 3.

A permanent, shallow thermocline underlies most of the region, shoaling to the east, with summer thermo-

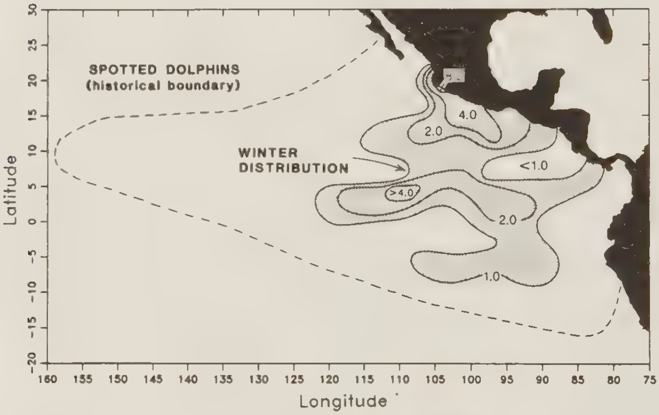
SPOTTED DOLPHINS
(historical boundary)
WINTER
DISTRIBUTION
4.0
2.0
<1.0
>4.0
2.0
1.0
Latitude
30
25
20
15
10
5
0
-5
-10
-15
-20
160
155
150
145
140
135
130
125
120
115
110
105
100
95
90
85
80
75
Longitude

Fig. 1. *Stenella attenuata* and *S. longirostris*. Spotted and spinner dolphin historical distribution boundary (shown dashed; from Perrin et al. 1983) and winter relative densities (shown as continuous contours of no. schools sighted per 185 km searched; from Au & Perryman 1985)

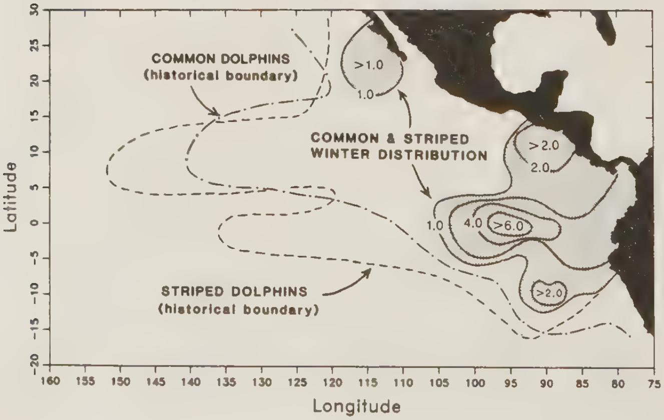
COMMON DOLPHINS
(historical boundary)
>1.0
1.0
COMMON & STRIPED
WINTER DISTRIBUTION
>2.0
2.0
1.0
4.0
>6.0
>2.0
STRIPED DOLPHINS
(historical boundary)
Latitude
30
25
20
15
10
5
0
-5
-10
-15
-20
160
155
150
145
140
135
130
125
120
115
110
105
100
95
90
85
80
75
Longitude

Fig. 2. *Stenella coeruleoalba* and *Delphinus delphis*. Striped and common dolphin historical distribution boundaries (from Perrin et al. 1983) and winter relative densities (contours of no. schools sighted per 185 km searched; from Au & Perryman 1985)

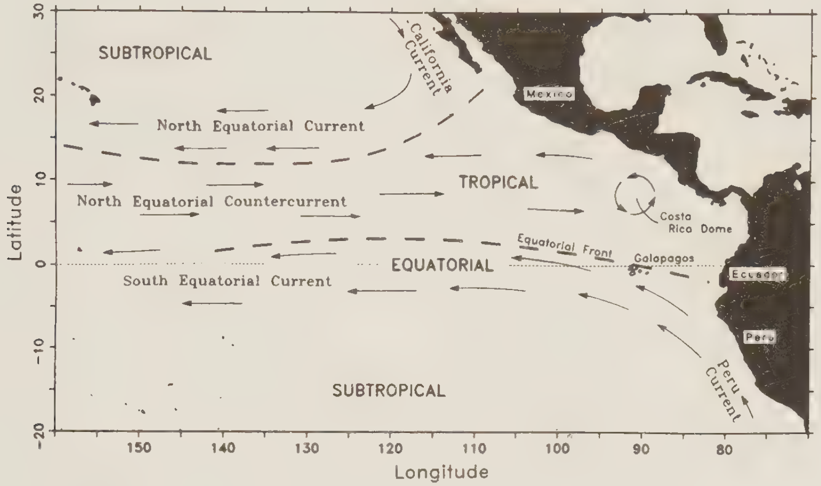

Fig. 3. Schematic representation of the surface water masses and surface circulation of the eastern tropical Pacific, adapted from Wyrtki (1966, 1967)

clines forming in subtropical and eastern equatorial waters. Biological productivity is enhanced by vertical nutrient flux to the euphotic zone along the zonal divergences (the equatorial upwelling and 10° N thermocline ridge; Love 1972), at the Costa Rica Dome (a quasi-permanent cyclonic eddy near 9° N and 89° W; Wyrtki 1964, King 1986), and through zonal advection from coastal upwellings (e.g. the Gulf of Tehuantepec; Owen & Zeitschel 1970). Secondary and higher level productivity and standing stocks are generally high in areas of high primary productivity (Blackburn et al. 1970). One of McGowan's (1974) Pacific Ocean 'biotic provinces' lies within these boundaries, maintained in part by recirculation of water due to the countercurrent systems. The historical distributions of spotted and spinner dolphins within the ETP (Fig. 1) clearly coincide in shape and location with the ETP Biotic Province.

Within this and other large oceanic regions, the abundance of animals from plankton to large nekton is patchy on a variety of spatial and temporal scales (Haury et al. 1978), with major consequences for the ecology of pelagic predators (e.g. Carr 1987). Large-scale aggregation of organisms known to be potential prey for pelagic dolphins (cephalopods, meso- and epipelagic fishes; Perrin et al. 1973) can be expected to occur along the equatorial front, and perhaps also around the Costa Rica Dome's upwelling (Owen 1981). Beebe's (1926) classical description of biological activity along a front was recorded at the equatorial front east of the Galapagos. Au & Perryman (1985) found some though not all spotted and spinner dolphin schools in the immediate area aligned along this front, just within the tropical waters.

Seasonality. Variability in surface circulation is primarily wind driven (Wyrtki 1974), so that processes and features affected by circulation (e.g. convergences and divergences) vary seasonally in response to shifting of the major wind systems. Wyrtki (1966, 1974) describes 2 oceanographic seasons in the eastern tropical Pacific. During January to June ('winter') the NE trade winds are strongest and in their most southerly position. At this time the North Equatorial Current (NEC) and opposing North Equatorial Counter Current (NECC) are weakest, as the trades are centered south of the NEC and act against the NECC.

In the second half of the calendar year ('summer') as the Intertropical Convergence Zone (where the NE and SE trade winds meet) moves northward from its winter minimum latitude near the equator, the NE trades are centered over and more strongly affect the NEC, and with lessened opposition from the wind, the NECC becomes stronger and is well developed from west of the dateline to near the coast of Central America. The NEC-NECC divergence is strongest at this time, so that the thermocline ridge near 10° N rises to within 40 m of the surface. The SE trades, the Peru Current and the SEC strengthen during the summer, producing greater equatorial upwelling and horizontal transport from the Peru Current.

Seasonal biological changes have not been demonstrated unequivocally for most of the ETP (Blackburn 1981, Vinogradov 1981). The cephalopods and fishes that are potential dolphin prey actively avoid standard net tows used to assess their distribution and abundance (e.g. Clarke 1977), obscuring possible seasonal cycles in existing data.

DATA AND METHODS

Data sources. Data from 18 research vessel ship-months from 1982, 1986 and 1987 (Table 1) were combined to examine 'summer' dolphin distributions. The 1986 and 1987 cruises were the first 2 of a 6 yr program to monitor trends in abundance of ETP dolphins. The cruise tracks were designed to cover the historical range of spotted dolphins in the ETP (the most widely distributed of the 4 species affected by the tuna fishery), stratified by previous density indices (Holt et al. 1987). The cruises used here (Fig. 4) surveyed 49 102 km (Table 1) during daylight hours in which there were functional sighting conditions (Beaufort 4 or less). The surveys were conducted at 10 knots (18.5 km h^{-1}), with 2 observers simultaneously on watch, each covering one side of the ship using a pair of 25× binoculars to search an arc from the ship's bow to about 100° to the beam (Holt & Sexton 1990). Dolphin sightings were approached for species identification and estimation of numbers within schools. Line transect abundance estimates from the 1986 and 1987 cruises were reported by Holt & Sexton (1989, 1990).

Mapping distribution patterns. To allow examination of spatial patterns within the region, and for direct comparability with Au & Perryman's (1985) winter distribution maps, their methods were followed (with exceptions noted below) for computing relative abundance as encounter rates (schools encountered per 185 km searched – the approximate distance searched in 1 d). The use of encounter rates to index relative abundance requires an assumption of no major spatial gradients in school size; this is generally consistent with available data (Holt et al. 1987). Au & Perryman (1985) computed moving averages of 5° lat.-long. blocks to smooth their data, then drew contours by hand. I used the commercial graphics package PLOT88 (Young & Van Woert 1987; algorithms ZGRID, SZMTH and ZCSEG) to smooth data in 2° lat.-long. blocks twice and then perform Laplacian interpolation of the smoothed fields. I included only blocks with at least 185 km search effort.

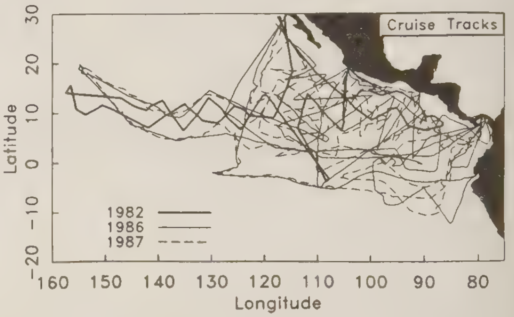

Fig. 4. Cruise tracks of research vessels during summer and fall 1982, 1986 and 1987 (used in this analysis)

Also following Au & Perryman (1985) data were combined for spotted and spinner dolphins, including in the same category schools where they occurred alone or together. These species are frequently sighted in mixed schools (73 % of spinner dolphin sightings also included spotted dolphins; Table 1), and not surprisingly their historical (Perrin et al. 1983) and winter (Au & Perryman 1985) distributions are quite similar. In contrast to Au & Perryman (1985) data were not combined for common and striped dolphins. While the areas of highest density for these species are similar (Au & Perryman 1985, this study) they are different in some important ways, described later.

Tests of water mass and thermocline topography as habitat indices. To examine the summer patterns in dolphin sightings in relation to surface water mass characteristics, sigma-t values (a measure of seawater density; see Pickard & Emery 1982) were computed from surface temperatures and salinities recorded continuously as the vessels traveled. The ships were equipped with ODEC TSG-102 Thermo-salinographs, which sampled temperature with a resolution of 0.1 °C, and salinity with a resolution of 0.01 Practical Salinity Units.

Table 1. Research vessel sighting effort (distance searched) and sightings of dolphin schools recorded during summer and fall 1982, 1986 and 1987 cruises

Date	km searched	No. schools of:						Total
	(n mile)	Spotted	Spotted & Spinner	Spinner	Spotted and/or Spinner	Striped	Common	
1982 Jun–Jul	7 708 (4 818)	22	38	5	65	23	12	100
1986 Aug–Nov	21 845 (13 653)	86	80	36	202	157	52	411
1987 Aug–Nov	19 549 (12 218)	94	75	30	199	184	33	416
Total	49 102 (30 658)	202	193	71	466	364	97	927

For graphic display, temperature and salinity data were averaged within 2° blocks, smoothed and interpolated, following the methods used to compute and display dolphin encounter rates.

Intermittent problems with the thermo-salinograph on the 1982 cruise resulted in the absence of data for many areas surveyed that year, and a bias in spatial coverage. Consequently, data from 1982 were not included in the following statistical analyses, and the sample size for these analyses was the sum of the 1986 and 1987 observations (827) from Table 1.

To examine relationships with thermocline topography I used depths of the 20 °C isotherm (Z20, commonly used to indicate location of the thermocline in the tropical Pacific; Hansen & Herman 1988) taken from XBTs deployed 4 to 6 times daily (every 55 to 110 km), and other XBTs deployed in the vicinity as reported to NOAA's National Ocean Survey (SEAS Office, N/OS1, 6001 Executive Blvd., Rockville, MD 20852, USA). For statistical comparisons with dolphin distributions, the 2° block mean values for sigma-t and Z20 were assigned to each of 827 sightings according to the 2° block in which they were recorded.

Univariate (ANOVA) and multivariate analysis of variance (MANOVA) were used to test the continuous distributions of sigma-t and Z20 for significant differences among sighting locations for 3 types of dolphin school: spotted and spinner (all sightings combined), common, and striped dolphins. Success in classifying the sightings to dolphin school type based on these habitat variables was judged by discriminant analysis (e.g. Cooley & Lohnes 1971), with school types as a priori groups.

As a check on the significance of the univariate and multivariate F-ratios, and the classifications from the discriminant analysis, these were compared to results expected from a random assortment of the sightings, using Monte Carlo methods (Hope 1968, Hair et al. 1987). This verification was done by randomly assigning each case (sighting with associated sigma-t and Z20 values) to one of the 3 school types, with overall proportions as in the original data (ca 10 % common, 41 % striped and 49 % spotted and spinner). The randomized data set was then tested by ANOVA and MANOVA for significant habitat differences among the pseudo-school types, followed by a classification of cases based on their discriminant function scores. This entire process was repeated 1000 times (Hope 1968) to produce reference sets of random uni- und multivariate F-ratios and classification results. The original F-ratios and classification results were then compared with these reference sets to assess the probability that the originals could have been obtained at random (i.e. Type I statistical error).

It was possible to test for seasonal differences in the sigma-t values of areas where the 3 school types were seen, because Au & Perryman (1985) gave a table reporting frequencies of sightings by sigma-t intervals. I could not conduct a similar test for Z20 seasonal differences because they did not publish such data for the winter sightings.

All statistical analyses were conducted with the commercial software package SYSTAT (Wilkinson 1988).

RESULTS

Summer geographic distributions

Differences between winter distribution patterns from Au & Perryman (1985) and the summer patterns reported here are apparent for spotted/spinner dolphins and striped dolphins. No seasonal changes are apparent for common dolphins.

In the summer data, spotted and spinner dolphin distribution extended westward along 10 °N (Fig. 5a), similar to their historical range (Fig. 1). The zonal lobe along 4 °N between 90 and 120 °W, described by Au & Perryman (1985) as prominent in winter (Fig. 1) was very weak during summer. During both winter and summer the area of highest abundance was off southern Mexico, with low abundance between the coast of South America and the Galapagos Islands. The winter lobe centered at 6 °S was nearly absent in summer. Striped dolphin distribution also extended offshore in the summer data (Fig. 5b), similar to the historical boundary (Fig. 2), but in a relatively patchy pattern.

There appears to be little seasonal change in common dolphin distribution. Their abundance centers in summer (Fig. 5c), as in winter (Fig. 2), were relatively coastal, along Baja California and extending offshore to near the Revillagigedos Is. (about 115 °W and 20 °N), along the coast of Ecuador where the Peru Current extends to the northwest, and in a very localized center in the vicinity of the Costa Rica Dome. Common dolphins are occasionally sighted far offshore (Fig. 1), but the effort-corrected data for both the summer and winter show that they occur much less frequently outside of the coastal areas and the equatorial zone east of about 100 °W (Figs. 2 and 5c). The areas where the 3 school types were most abundant (contours of 2 or more schools sighted per 185 km searched) were spatially separated, with a few exceptions (Fig. 5).

Water mass and thermocline depth as habitat indices

There was considerable overlap among dolphin school types in the occupied ranges of both surface density and thermocline depth values (Fig. 6), but the

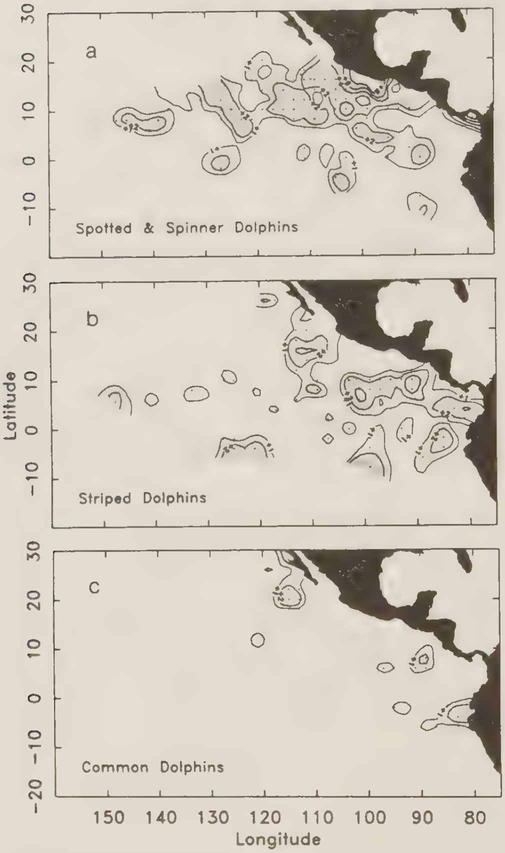

Fig. 5. Summer dolphin distributions in the ETP (contours of encounter rates per 185 km searched). Dots represent centers of 2° squares in which there was at least 185 km search effort. (a) Spotted plus spinner dolphins; (b) striped dolphins; (c) common dolphins

means for both variables were significantly different among the 3 school types, as detailed below.

Water mass characteristics

In the summer, spotted and spinner dolphins occupied the most tropical water of the species examined here (sigma-t mean = 21.2, SE = 0.071, n = 401, CV = 6.7 %). Common dolphins occupied less tropical areas on average (mean sigma-t = 22.2, SE = 0.183, n = 85, CV = 7.6 %), but this frequency distribution is bimodal, so a mean or other measure of central tendency is of limited value. Striped dolphins were found in areas that are, on average, intermediate between means for the other species (sigma-t mean = 21.6, SE = 0.073, n = 341, CV = 6.3 %). The 3 means are significantly different (Table 2), but this result alone is inconclusive because the ANOVA assumptions of normality (Fig. 6) and homogeneity of variances are violated. However, results of the Monte Carlo runs supported the conclusion of a very low Type I error ($p < 0.001$). The largest F-ratio from the 1000 runs was just 6.8, as compared to the 16.9 observed.

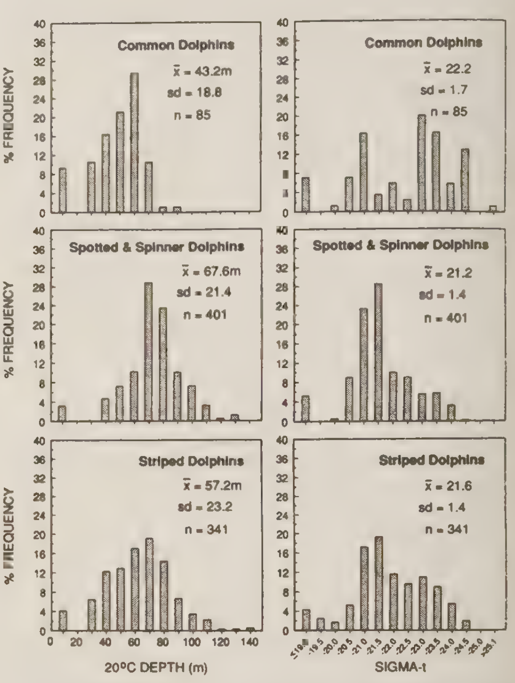

Fig. 6. Frequency histograms, transformed to percentages, of surface water density (sigma-t) and 20 °C isotherm depths (m) (Z20) in areas where dolphins were sighted, by dolphin school type

Thermocline characteristics

Spotted and spinner dolphins were sighted in areas with thermoclines relatively deeper than the other 2 species, but intermediate for the entire region (Z20 mean = 67.72 m, SE = 1.066, n = 401, CV = 32 %). Common dolphins were seen, on average, in areas with shallower thermoclines (Z20 mean = 43.16 m, SE = 2.037, n = 85, CV = 44 %). This includes areas where the 20 °C isotherm breaks the surface due to upwelling. Striped dolphins were found in waters with thermocline depths intermediate between these, on average (Z20 mean = 57.20 m, SE = 1.256, n = 341, CV = 41 %). The standard errors of means reported above are

Table 2. Analyses of variance testing the null hypothesis of no differences among dolphin school types in water mass (sigma-t) and thermocline depth (indexed by depth of 20 °C isotherm, Z20) of their sighting locations

Univariate analyses Source	SS	df	MS	F	p	p_{MC}[a]
Sigma-t	68.846	2	34.423	16.9	< 0.001	< 0.001
Error	1677.329	824	2.036			
Z20	49507.278	2	24753.639	51.7	< 0.001	< 0.001
Error	394919.027	824	479.271			
Multivariate analyses						
Wilke's lambda[b] = 0.840		Rao's F[b] = 37.487			$p < 0.001$	p_{MC}[a] < 0.001

[a] p-values from comparisons to Monte Carlo simulations

[b] Multivariate statistics defined as in Cooley & Lohnes (1971)

all quite small, a result of sample sizes being relatively large (85 to 401). These 3 means are significantly different (Table 2). As with the sigma-t univariate test, the Monte Carlo results appear to verify the very low Type I error. The largest F-ratio of the 1000 run reference set was just 9.1.

Multivariate analyses

The dolphin school types occupied significantly different habitats, defined by the joint Z20 and sigma-t continuous distributions of their sighting localities. That is, a MANOVA resulted in rejection of the null hypothesis of no differences among school types (Table 2). Classification of individual sightings to dolphin school type from their discriminant function scores resulted in the following success rates: spotted/spinner, 66 %; common, 64 %; striped, 24 % (Table 3).

Table 3. Classification table from discriminant analysis of dolphin school types by habitat variables (sigma-t and Z20, depth of the 20 °C isotherm). Successful classifications are represented on the diagonal

	Predicted group			
Actual group	Common	Spotted/ spinner	Striped	Totals
Common	**54** **(63.5)**	11 (13.0)	20 (23.5)	85 (100 %)
Spotted/ spinner	45 (11.2)	**266** **(66.4)**	90 (22.4)	401 (100 %)
Striped	125 (36.7)	134 (39.3)	**82** **(24.0)**	341 (100 %)
Totals	224	411	192	827

In 1000 runs of the Monte Carlo procedure, a significant difference among the 3 randomized groups ($p \leq 0.05$ for the multivariate F) occurred only twice (0.2 %). No multivariate F values from the simulations exceeded that observed for the actual data (37.5), verifying the conclusion that the probability of Type I error was less than 0.001.

Similarly, the school type classifications from the 1000 randomized (Monte Carlo) Discriminant Analyses appear to verify the classifications actually observed, but only for 2 of the 3 school types. For spotted and spinner dolphins, the mean 'hit score' of the reference set was 42.7 %. Only 4 of 1000 runs had scores exceeding the 63.5 % actually observed (probability of Type I error = 0.004). For common dolphins, the mean hit score of the reference set was just 32.2 %. None of the 1000 runs had scores greater than the 66.3 % actually observed ($p < 0.001$). For striped dolphins, the mean hit score of the reference set was 32.6 %. The observed score of 24 % is not significantly different from this mean ($t = 0.67$, $p = 0.57$), indicating that we could do as well at correctly classifying striped dolphin sightings by random guessing, without considering the habitat data.

Seasonal contrast

During the summer all 3 dolphin types had significantly different sigma-t distributions as compared with their winter distributions from Au & Perryman (1985) ($p < 0.001$ for all 3 tests). The summer sigma-t distributions are shifted to lower values reflecting seasonal warming of surface waters.

DISCUSSION

Seasonal changes in geographic distribution

Seasonal changes in the locations of high density areas were observed for spotted, spinner and striped dolphins, but not for common dolphins. The most apparent change was the presence of high density areas west of 120° W along 10° N during the summer;

this was more prominent for spotted and spinner dolphins, less so for striped. Concomitant with the presence of this summer density center for spotted and spinner dolphins was the absence of the winter high density areas along 4° N between 90 and 120° W, and along 6° S between 88 and 110° W. One hypothesis suggested by these complementary changes is an intraregional, seasonal movement. The distance from the approximate center of the winter area along 4° N to the center of the summer area along 10° N is over 2500 km, consistent in direction but about twice the maximum distance observed in the limited amount of available mark-recapture data (Perrin et al. 1979, Hedgepeth 1985). A population movement between the western and southern parts of the region is also consistent with patterns of intraspecific morphological variability (Perrin et al. 1985), which indicate more similarity between spotted and spinner dolphins from these western and southern areas than between individuals from either area and those from the high-density center off Mexico.

The observed seasonal changes in dolphin distribution are at least partially explainable in light of seasonal changes in the atmosphere and ocean. The offshore extension along 10° N of spotted, spinner and striped dolphins in the summer clearly coincides with the northward movement of the Intertropical Convergence Zone, the subsequent increase in flow of the NEC and NECC and shoaling of the thermocline ridge at their divergence. Spotted, spinner and striped dolphins appear to aggregate in this area when the thermocline shoals under the tropical surface water, approximating physical conditions occurring in the more nearshore, more densely occupied parts of their ranges east of 125° W.

The summer decrease in spotted and spinner dolphin abundance at the density center along 6° S also coincides with a major seasonal oceanographic change. During the northern summer the Peru Current and SEC are stronger and push farther north in the ETP, and the warm surface layer over the normally subtropical surface water, present in the winter when spotters and spinners are abundant there, recedes to the north. Spotted and spinner abundance was lower during the period of cool, subtropical conditions south of the equator.

The seasonal variation in spotted and spinner distribution occurs in the southern and western parts of the ETP. The triangular, high-density area off Mexico is in the same location, and has the highest density of schools, during both winter and summer. This is the most tropical part of the ETP and has the least seasonally variable oceanography conditions of the region (Wyrtki 1965b, 1974).

Common dolphin distribution does not undergo major seasonal shifts in the ETP. The locations of the year-round density centers best fit Au & Perryman's (1985) description of 'upwelling modified' habitat, being localized near the Revillagigedos Is., along the coast of Baja California and Ecuador, and near the Costa Rica Dome.

If seasonal variations in biological productivity along the 10° N thermocline ridge are small (and perhaps not verified), what accounts for the substantial seasonal variation in dolphin abundance there? It may be related to seasonal change in availability, rather than abundance, of their prey. The shallow thermocline may act as a vertical aggregating mechanism and barrier to rapid escape by the squids and fishes dolphins prey upon (Green 1967) so that when the thermocline reaches some minimum depth range, spotted, spinner and striped dolphins can successfully forage there. During the summer this area is also an important part of the distribution of surface-schooling yellowfin tuna (Calkins 1975), which forage similarly to (and frequently with) these dolphin species.

As noted by Au & Perryman (1985) the winter density center along 4° N coincides in location with a major zonal convergence at the meeting of the NECC and SEC. This convergence is thought to form the equatorial front (Pak & Zaneveld 1974), and consequent aggregation of potential dolphin prey (e.g. Sette 1955, Murphy & Shomura 1972, Greenblatt 1979). However, the prey aggregation hypothesis is not strongly supported by the seasonal change in dolphin abundance here, as this convergence zone is less abundantly occupied by spotted and spinner dolphins during the summer, when frontal structures are best developed. Perhaps during stronger upwelling periods there is insufficient time for development of an abundant dolphin prey community during the transit of water to the convergence zone (Le Fevre 1986).

Dolphin habitats

The spatial separation of density centers for spotted and spinner dolphins from centers for common and striped dolphins, reported by Au & Perryman (1985) for the winter months, appears to be a year-round pattern. While the locations of some density centers varied from winter to summer, there was still separation among species. I also found striped dolphin distribution in the summer to be spatially different from common dolphin distribution, in contrast to the winter condition reported by Au & Perryman (1985).

The distribution of 2 of the 3 school types (spotted/spinner; common dolphins) were statistically separable based on thermocline depth and surface water density. This is consistent with the spatial separation of high density centers, and indicates moderate success in indexing physical habitats for these ETP dolphins, at least on the spatial and temporal scales of this study.

Striped dolphin distribution was found to be intermediate between the distributions of common and spotted/spinner dolphins, both qualitatively and quantitatively. While the univariate means and multivariate centroids of Z20 and sigma-t were statistically different from those for the other species, these statistical differences are probably not ecologically meaningful. This is emphasized by the clear lack of success in post-classifying striped dolphin sightings based on Z20 and sigma-t. That is, the spatial separation of striped dolphin density centers from centers for the other dolphin school types (Fig. 5) was not reflected robustly in the multivariate statistical analyses of habitat characteristics. This suggests that other processes, not directly related to physical habitat as defined and measured here, act to separate these dolphins from the others.

Other statistical comparisons of ETP cetacean distribution and environmental variables were made by Reilly (1977) and Polacheck (1987). Both studies used sightings from observers on tuna vessels and climatological oceanographic data, summarized in 5° blocks. Both produced statistically equivocal results, probably resulting from the biased searching of tuna vessels in relation to dolphin distributions (Edwards 1989, Edwards & Kleiber 1990), the lack of precision inherent in climatologies, and the large spatial units used. However, Polacheck's (1987) results for spotted and spinner dolphins were generally consistent with those of Au & Perryman (1985) and this study regarding gross spatial patterns, and the existence of some underlying associations between physical environmental variables and dolphin distribution.

Caveats

Many of the smaller details of the maps may reflect data collection and processing as much as the true shape of the distributions. Pooling data into 2° lat.-long. blocks imposed a minimum level of resolution on the results. Smoothing and interpolation necessary to produce fields appropriate for study of regional patterns is done at the expense of fine-scale detail. If dolphin school types separate on spatial scales smaller than that examined here (which has been the author's personal observation) this separation would not have been detected in the maps or statistical analyses.

Inter-annual variation is another possible source of error here. It is possible that the number of years sampled in both the winter series (4 by Au & Perryman 1985) and summer series (3 by this study) were not sufficient to fully represent 'typical' seasonal patterns. We will examine patterns of interannual variation in summer dolphin distribution at the close of the 6 yr sampling program in 1992. We are also investigating meso- and smaller scale patterns of sightings and contemporaneously measured environmental properties to determine the scale dependency (e.g. Schneider & Duffy 1985) of dolphin distributions and physical habitat.

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LITERATURE CITED

Au, D. W. K., Perryman, W. L. (1985). Dolphin habitats in the eastern tropical Pacific. Fish Bull. U.S. 83 (4): 623–643

Beebe, W. (1926). The *Arcturus* adventure. Putnam & Sons, New York

Blackburn, M. (1981). Low latitude gyral regions. In: Longhurst, A R. (ed.) Analysis of marine ecosystems. Academic Press, New York p. 3–29

Blackburn, M., Laurs, R. M., Owen, R. S., Zeitschel, B. (1970). Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. 7: 14–31

Calkins, T. P. (1975). Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics, 1971–1974. Bull. inter-Am. trop. Tuna Commn 17: 1–116

Carr, A. (1987). New perspectives on the pelagic stage of sea turtle development. Conserv. Biol. 1 (2): 103–121

Clarke, M. R. (1977). Beaks, nets and numbers. Symp. zool. Soc. Lond. 38: 89–126

Condy, P. R., van Aarde, R. J., Bester, M. N. (1978). The seasonal occurrence and behavior of killer whales, *Orcinus orca*, at Marion Island. J. Zool., Lond. 184 (4): 449–464

Cooley, W. W., Lohnes, P. R. (1971). Multivariate statistical analysis. John Wiley & Sons, New York

Edwards, E. F. (1989). Using tuna vessel observer data to detect trends in abundance of dolphin populations: history and research to date (1988). NOAA tech. Memo., NMFS-SWFC-122

Edwards, E. F., Kleiber, P. M. (1990). Effects of nonrandomness on estimates of dolphin school abundance derived from tuna vessel observer data. Fish. Bull. U.S. (in press)

Evans, W. E. (1975). Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph. D. thesis, Univ. of Calif. Los Angeles

Gaskin, D. E. (1982). The ecology of whales and dolphins. Heinemann, London

Green, R. E. (1967). Relationships of the thermocline to success of purse seining for tuna. Trans. Am. Fish. Soc. 96: 126–130

Greenblatt, P. R. (1979). Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull. U.S. 77: 147–155

Hair, J. F. Jr., Anderson, R. E., Tatham, R. L. (1987). Multivariate data analysis with readings. Macmillan, New York

Hansen, D. V., Herman, A. (1988). A seasonal isotherm depth climatology for the eastern tropical Pacific. NOAA tech. Rep. 434-AOML 33 (Revised)

Haury, L. R., McGowan, J. A., Wiebe, P. H. (1978). Patterns and processes in the time-space scales of plankton distributions. In: Steele, J. H. (ed.) Spatial pattern in plankton communities. Plenum Press, New York, p. 277–327

Hedgepeth, J. B. (1985). Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Southwest Fisheries Center Admin. Rept. No. LJ-85-03, p. 1–40

Holt, R. S., Gerrodette, T., Cologne, J. B. (1987). Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull. U.S. 85 (3): 435–446

Holt, R. S., Sexton, S. N. (1989). Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analysis of 1987 data. Rep. int. Whal. Commn. 39: 347–351

Holt, R. S., Sexton, S. N. (1990). Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. Fish. Bull. U.S. 88 (1): 105–111

Hope, A. C. A. (1968). A simplified Monte Carlo significance test procedure. J. R. statist. Soc. Ser. B 30 (3): 582–598

Jonsgard, A., Lyshoel, P. B. (1970). A contribution to the knowledge of the biology of the killer whale. Norw. J. Zool. 18: 41–48

King, F. D. (1986). The dependence of primary production in the mixed layer of the eastern tropical Pacific on the vertical transport of nitrate. Deep-Sea Res. 33 (6): 733–754

Le Fevre, J. (1986). Aspects of the biology of frontal systems. In: Blaxter, J. H. S., Southward, A. J. (eds.) Advances in marine biology, Vol. 23. Academic Press, New York

Leatherwood, J. S., Walker, W. A. (1979). The northern right whale dolphin *Lissodelphis borealis* Peale in the eastern north Pacific. In: Winn, H. E., Olla, B. L. (eds.) Behavior of marine animals, Vol. 3: Cetaceans. Plenum Press, New York, p. 85–141

Love, C. M. (ed.) (1972). Biological and nutrient chemistry data from principal participating ships, second survey cruise, August–September 1967. EASTROPAC Atlas, Vol. 6. Natl. Mar. Fish. Serv., Circ. 330, p. 1–80

McGowan, J. A. (1974). The nature of oceanic ecosystems. In: Miller, C. B. (ed.) The biology of the oceanic Pacific. Oregon St. Univ. Press, Corvallis, p. 9–28

Mercer, M. C. (1975). Modified Leslie-DeLury population models of the long-finned pilot whale *(Globicephala melaena)* and annual production of the short-finned squid *(Illex illecebrosus)* based upon their interaction at Newfoundland. J. Fish. Res. Bd Can. 32: 1145–1154

Miyazaki, N., Kasuya, T., Nishiwaki, M. (1974). Distribution and migration of two species of *Stenella* in the Pacific coast of Japan. Sci. Rep. Whales Res. Inst., Japan 26: 227–243

Murphy, G. I., Shomura, R. S. (1972). Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull. U.S. 70 (3) 785–905

Owen, R. W. (1981). Fronts and eddies in the sea: mechanisms, interactions and biological effects. In: Longhurst, A. R. (ed.) Analysis of marine ecosystems. Academic Press, New York, p. 197–227

Owen, R. W., Zeitschel, B. (1970). Phytoplankton production: seasonal changes in the oceanic eastern tropical Pacific. Mar. Biol. 7 (1): 32–36

Pak, H., Zaneveld, J. R. V. (1974). Equatorial front in the eastern Pacific Ocean. J. phys. Oceanogr. 4: 570–580

Perrin, W. F. (1969). Using porpoise to catch tuna. Wld Fish. 18 (6): 42–45

Perrin, W. F. (1975). Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Bd Can. 32: 1059–1067

Perrin, W. F. (1988). Dolphins, porpoises and whales – an action plan for the conservation of biological diversity: 1988–1992. IUCN, Gland, Switzerland

Perrin, W. F., Warner, R. R., Fiscus, C. H., Holts, D. B. (1973). Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull. U.S. 71 (4): 1077–1092

Perrin, W. F., Evans, W. E., Holts, D. B. (1979). Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by the results of tagging operations, 1969–76. NOAA techn. Rep. NMFS SSRF-737, p. 1–14

Perrin W. F., Scott, M. D., Walker, G. J., Ralston, F. M., Au, D. W. K. (1983). Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, with an annotated catalog of data sources. NOAA techn. Memo NOAA-TM-NMFS-SWFC-38, p. 1–65

Perrin, W. F., Scott, M. D., Walker, G. J., Cass, V. L. (1985). Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA tech. Rep. NMFS 28, p. 1–28

Pickard, G. L., Emery, W. J. (1982). Descriptive physical oceanography. 4th (SI) enlarged edition. Pergamon Press, Oxford

Polacheck, T. (1987). Relative abundance, distribution and interspecific relationship of cetacean schools in the eastern tropical Pacific. Mar. Mammal Sci. 3 (1): 54–77

Reilly, S. B. (1977). The distribution of pilot whales, *Globicephala macrorhynchus* Gray, 1896, in the eastern tropical Pacific. M.S. thesis, Calif. Polytech. St. Univ., San Luis Obispo, California

Schneider, D. C., Duffy, D. C. (1985). Scale-dependent variability in seabird abundance. Mar. Ecol. Prog. Ser. 25: 211–218

Selzer, L. A., Payne, P. M. (1988). The distribution of white-sided *(Lagenorhynchus acutus)* and common dolphins *(Delphinus delphis)* vs. environmental features of the continental shelf of the northeastern United States. Mar. Mammal Sci 4 (2): 141–153

Sette, O. E. (1955). Consideration of mid-ocean fish production as related to oceanic circulatory systems. J. mar. Res. 14 (4): 398–414

Smith, T. (1983). Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull U.S. 81 (1): 1–13

Tomilin, A. G. (1967). Mammals of the USSR and adjacent countries. Vol. IX, Cetacea. Translation by Israel Program for Scientific Translation. Heptner, V. G. (ed.)

Tsuchiya, M. (1970). Equatorial circulation of the south Pacific. In: Wooster, E. (ed.) Scientific exploration of the South Pacific. Natl. Acad. Sci., Washington, D.C., p. 69–74

Tsuchiya, M. (1974). Variation of the surface geostrophic flow in the eastern intertropical Pacific Ocean. Fish. Bull. U.S. 72 (4): 1075–1086

Tsuchiya, M. (1982). On the Pacific upper-water circulation. J. mar. Res. (Suppl.) 40: 777–799

Viale, D. (1985). Cetaceans in the northwestern Mediterranean: their place in the ecosystem. Oceanogr. mar. Biol. A. Rev. 23: 491–571

Vinogradov, M. E. (1981). Ecosystems of equatorial upwellings. In: Longhurst, A. R. (ed.) Analysis of marine ecosystems. Academic Press, New York, p. 69–93

Wilkinson, L. (1988). SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Illinois

Wooster, W. S., Cromwell, T. (1958). An oceanographic description of the eastern tropical Pacific. Bull. Scripps Instn Oceanogr. 7: 169–282

Wyrtki, K. (1964). Upwelling in the Costa Rica Dome. Fish. Bull U.S. 63: 355–372

Wyrtki, K. (1965a). Surface currents in the eastern tropical Pacific Ocean. Bull. inter-Am. trop. Tuna Commn 9: 269–304

Wyrtki, K. (1965b). The annual and semiannual variation of the sea surface temperature in the North Pacific Ocean. Limnol. Oceanogr. 10 (3): 307–313

Wyrtki, K. (1966). Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. mar. Biol. A. Rev. 4: 33–68

Wyrtki, K. (1967). Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1: 117–147

Wyrtki, K. (1974). Sea level and the seasonal fluctuations of the equatorial currents in the western Pacific Ocean. J. Phys. Oceanogr. 4: 91–103

Young, T. L., Van Woert, M. L. (1987). PLOT88 software library. Plotworks, Inc., La Jolla, California

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BLUE WHALE (*BALAENOPTERA MUSCULUS*) DISTRIBUTION IN THE EASTERN TROPICAL PACIFIC

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Abstract

The distribution of blue whales, *Balaenoptera musculus,* in the eastern tropical Pacific (ETP) was analyzed from 211 sightings of 355 whales recorded during research vessel sighting surveys or by biologists aboard fishing vessels. Over 90% of the sightings were made in just two areas: along Baja California, and in the vicinity of the Costa Rica Dome (a large, stationary eddy centered near 9°N, 89°W), with the rest made along the equator near the Galapagos Islands, the coasts of Ecuador and northern Peru. All sightings occurred in relatively cool, upwelling-modified waters. Because these areas are the most productive parts of the ETP, and have relatively large standing stocks of euphausiids, it seems possible that blue whales select low latitude habitats which permit foraging. The waters off western Baja California were occupied seasonally, with a peak in sightings coinciding with the spring peak in upwelling and biological production. The Costa Rica Dome area was occupied year round, suggesting either a resident population, or that both northern and southern hemisphere whales visit, with temporal overlap. The modal group size was one for all areas and seasons, but the frequency of groups with two or more whales was significantly higher in sightings made near the Galapagos Islands and the coast of Ecuador and northern Peru.

Key words: blue whales, *Balaenoptera musculus,* distribution, oceanography, tropical Pacific.

Ecological aspects of blue whale distribution and feeding in high latitudes have been studied extensively from whaling operations (Beklemeshev 1960; Mitchell 1975; Nasu 1963, 1966; Nemoto 1957, 1959, 1970; Uda 1954; and others). The ecology of their distribution outside of the high-latitude whaling regions has been little studied (Gaskin 1982). A relative wealth of information on physical and biological oceanography of the eastern tropical Pacific (ETP)

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(*e.g.*, Blackburn 1968, Brinton 1979, Hansen and Herman 1988, Longhurst 1976, Love 1972, Wyrtki 1966), coupled with nearly 20 yr of sighting effort for cetaceans, provides an opportunity to study some aspects of blue whale distributional ecology in a tropical region.

Here we delimit the ETP oceanographically, following Wyrtki (1966), as comprising the Tropical, Equatorial and Transitional surface water masses of the eastern Pacific. These lie roughly within 25°N, 10°S, the American continents and 130°W.

The classical depiction of blue whale distribution (*e.g.*, Lockyer and Brown 1981, Mackintosh 1965) describes a seasonal migration between high latitudes, where they feed extensively and exclusively on euphausiids, and low latitudes where they mate and give birth, but do not feed. Since foraging has not been considered an important factor in their low latitude distribution (Mackintosh 1966), previously published information does not indicate what factors determine the choice of "winter" habitat.

While most blue whales are assumed to migrate to high latitudes during part of each year, data from both the Pacific and Indian Oceans indicate that some individuals may remain in low latitudes year round. Blue whales have been seen in all seasons off Peru (Donovan 1984) and in the Northern Hemisphere portions of the Indian Ocean (Yochem and Leatherwood 1985). Similarly, all individuals may not leave high latitudes each year; Kellogg (1929) reported sighting a few blue whales near South Georgia throughout the Antarctic winter.

When in temperate and tropical zones blue whales are known to occupy both pelagic and coastal shelf waters (Leatherwood and Reeves 1983, Yochem and Leatherwood 1985). In the eastern Pacific, blue whales have been reported from the Gulf of Alaska and near the Aleutian Islands (Nishiwaki 1966), in the mid-Pacific between 20°N and 35°N (Yochem and Leatherwood 1985), on and near the coastal shelves of North America (Kellogg 1929, Rice 1974, Scammon 1874) and South America (Aguayo 1974, Clarke 1980, Donovan 1984).

Whaling records from South American land stations indicate that blue whales were rarely captured north of about 30°S in the Peru Current (Clarke 1980, Mackintosh 1965), but Donovan (1984) reported 10 sightings made in two days between 4°S and 8°S within about 100 km of the coast. The Baja California peninsula and Gulf of California are known as gathering places for relatively large numbers of blue whales with peak abundance during the northern spring (Rice 1974; Sears 1987; Vidal *et al.*, in press).

Few blue whale sightings have been reported for the tropical Pacific. Their absence off Baja California during November through January in Rice's (1974) data caused him to surmise that they had either moved south into Tropical waters, or west. Wade and Friedrichsen (1979) reported 20 sightings in the northern winter in the ETP (from the same sources included here), 19 of which were very localized off Central America near a major oceanic eddy, the Costa Rica Dome, centered near 9°N, 89°W (Wyrtki 1964). They cited previous blue whale sightings made there in 1928 (Kellogg 1929), and sightings at this location of unidentified rorquals made in 1975 (Volkov and Moroz 1977). Having data from only one season, Wade and Friedrichsen (1979) interpreted this to be a wintering area, but noted that the high standing stock of zooplankton reported for the Costa Rica Dome may also permit feeding.

Berzin (1978) identified 24 of the rorquals cited by Volkov and Moroz (1977) off Central America as blue whales. From the sightings of blue whales off Central America during both March and June of 1975, Berzin (1978) speculated that they may represent a resident population. While two sets of sightings made two and one half months apart are weak grounds for such speculation, our results indicate that Berzin may well have been correct.

In this study we report 211 sightings of 355 blue whales in the ETP made during 1975–1988, and discuss seasonality, habitats occupied, and potential population structure for the region, including the possibility that a year-round occupation of the Costa Rica Dome area represents a resident population. We did not attempt an estimate of absolute abundance, feeling that to be beyond the scope of our data.

MATERIALS AND METHODS

We compiled sightings of blue whales made in the ETP from two sources: (1) research vessel sighting surveys conducted by the U.S. National Marine Fisheries Service (NMFS) since 1974 specifically to search for cetaceans, and (2) sightings made by NMFS scientific observers on commercial tuna fishing boats operating in the ETP since 1968 and by Inter-American Tropical Tuna Commission observers since 1977. Beginning in 1975 the tuna vessel observers recorded data on vessel operations, allowing computation of an approximate index of searching effort (km traveled while searching). Research vessel searching effort has been recorded in detail (*e.g.,* Holt and Sexton 1989). Sightings and search effort were combined from both platform types, comprising 211 sightings made during 12,175,200 km searching in good sighting conditions (Beaufort 4 or less) and all months of the year.

Observers on both platform types were trained in cetacean field identification and recorded (at minimum) identifying characteristics, date and location of sighted animals. Nominal blue whale sightings were verified twice. First, upon return of an observer from a cruise all cetacean sightings were screened by data editors to see if minimal characteristics were recorded to provide identification to the species level. Second, we reviewed each sighting at the onset of this study for consistency of identification criteria (following Leatherwood and Reeves 1983). We also screened the sightings for possible duplicates—a concern given the vast amount of search effort included here—and found none.

The research vessels typically approached all sighted schools of small cetaceans and most large cetaceans to allow identification and counting of numbers present. The tuna vessels rarely diverted for large whale sightings because their targets were fish and dolphins, so that most large whales seen from these vessels were not identified unless close enough to the vessel for the scientific observer to examine them with hand-held binoculars. We assume this negative bias in representing absolute abundance to be constant throughout the year and for all parts of the ETP, so that tuna vessel observer data, like research vessel data,

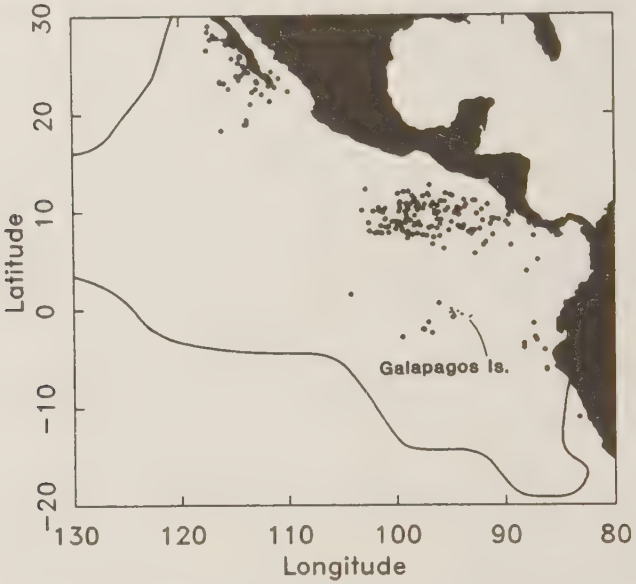

Figure 1. Spatial distribution of 211 blue whale sightings in the eastern tropical Pacific, 1974–1988. The boundary line encloses the area in which there was at least 185 km search effort per one degree latitude–longitude block.

provide an unbiased representation of spatial and seasonal distribution patterns for blue whales.

Relative densities of blue whales were computed for one-degree latitude–longitude blocks. Density estimates were calculated as whales seen per km searched during periods of good sighting conditions (Beaufort 4 or less), in one-degree squares for which there was at least 185 km searching effort. This minimum effort level was selected following Polacheck's (1983) sensitivity analyses of tuna vessel observer data for estimating cetacean encounter rates. Relative density estimates were made by calendar quarters, pooled over 1975–1988, to examine intra-annual variation. There were too few sightings per year to allow meaningful examination of inter-annual variation.

Group size estimates were analyzed by sub-areas within the ETP, to test for intra-regional differences, using contingency table analysis with all sightings of three or more pooled into one category.

RESULTS

All sightings were made within three (or perhaps four) relatively small areas (Fig. 1), while a much larger total area was searched with at least the minimum amount of effort (Fig. 2). The largest subset consists of 150 sightings made off Central America in a distinct aggregation bounded by 85°W–10°W, and about 6°N–13°N, centered near the Costa Rica Dome. An aggregation of 43 sightings

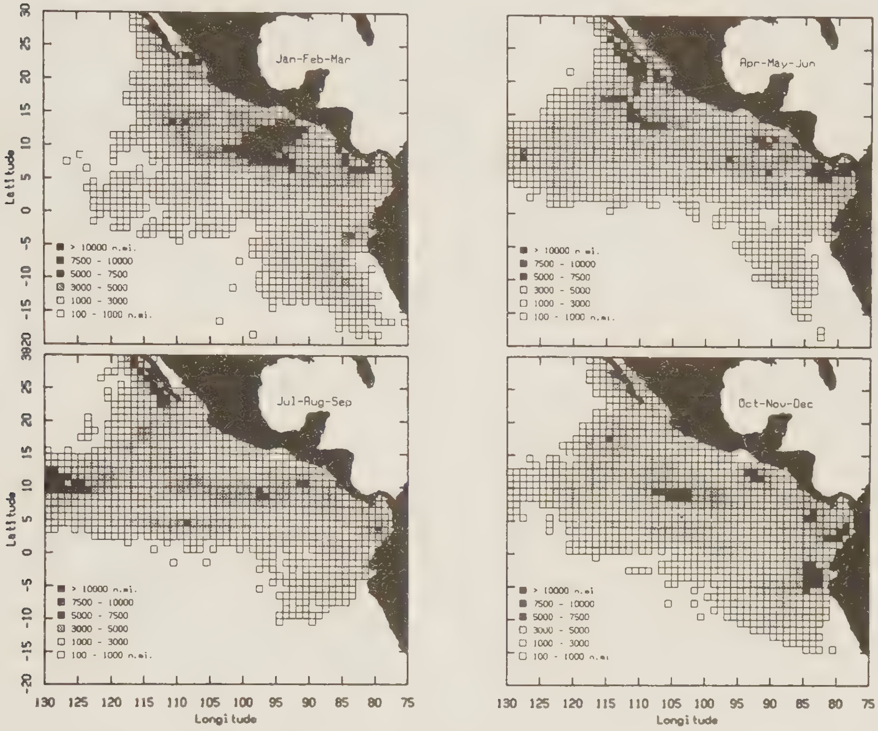
Jan-Feb-Mar
Apr-May-Jun
Jul-Aug-Sep
Oct-Nov-Dec
> 10000 n.mi.
7500 - 10000
5000 - 7500
3000 - 5000
1000 - 3000
100 - 1000 n.mi.
Latitude
Longitude
30
25
20
15
10
5
0
-5
-10
-15
-20
130
125
120
115
110
105
100
95
90
85
80
75

Figure 2. Searching effort for cetaceans in the eastern tropical Pacific, by calendar quarter, 1975–1988. Data are combined from research vessel surveys and from scientific observers onboard tuna purse seiners. Only one degree latitude–longitude blocks with at least 185 km (100 n. mi.) searching are included.

occurred along Baja California. Smaller numbers of sightings were made off Ecuador and northern Peru (11), and near the Galapagos Islands (7).

The aggregation off Central America occurred during all four calendar quarters (Fig. 3), but was most dense during January–March, when it was also distinctly separated from the coast. During the second and third quarters there was an apparent shift to the east, with more sightings made near the coast, and very few made west of 95°W.

Blue whale sightings near Baja California varied seasonally (Fig. 3). During April–June, sightings were made from south of Cabo San Lucas to north of 25°N, the northern limit of the study area. Very few blue whales were seen there during July–September. During October–March blue whales were observed off Baja California, but only near the southern tip, and a little farther south near the Revillagigedo Islands (near 19°N, 111°W). The few sightings made along the equator and near the coast of South America may represent one or two aggregations.

The modal group size recorded for all seasons and aggregations was one, with single whales accounting for 67% of the sightings. There was a significant

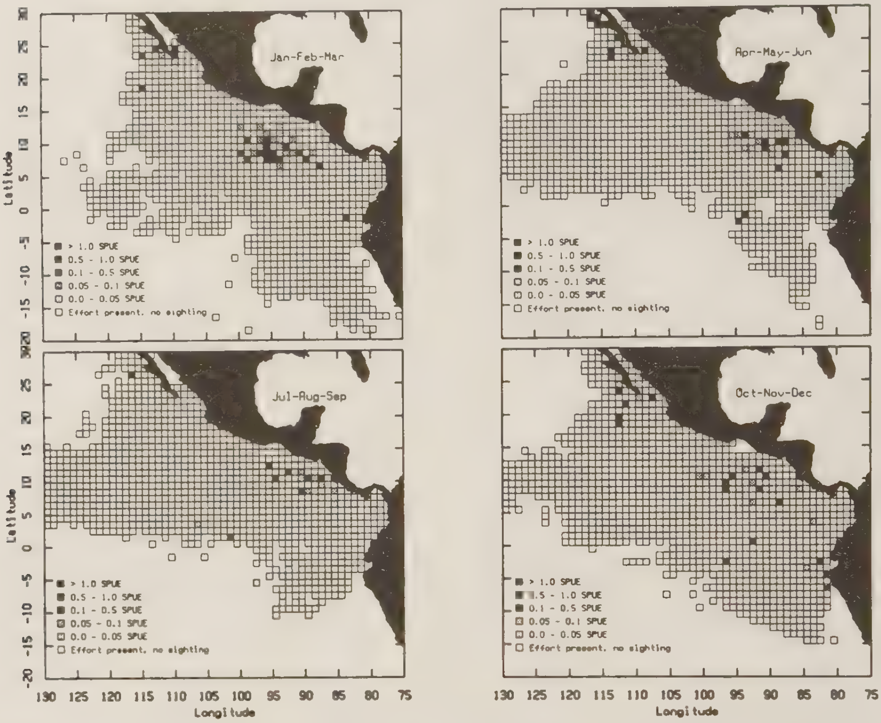
Jan-Feb-Mar
Apr-May-Jun
Jul-Aug-Sep
Oct-Nov-Dec
Latitude
Longitude
30 25 20 15 10 5 0 -5 -10 -15 -20
130 125 120 115 110 105 100 95 90 85 80 75
> 1.0 SPUE
0.5 - 1.0 SPUE
0.1 - 0.5 SPUE
0.05 - 0.1 SPUE
0.0 - 0.05 SPUE
Effort present, no sighting

Figure 3. Relative abundance of blue whales (sightings per 370 km searched during periods of Beaufort 4 or lower) by calendar quarter: a) Jan–Feb–Mar; b) Apr–May–Jun; c) Jul–Aug–Sep; d) Oct–Nov–Dec. Only one degree latitude–longitude blocks with at least 185 km (100 n. mi.) searching are included.

difference in the group size frequency among the aggregation areas (Table 1). A partitioning of the chi-square statistic indicates that the largest departures from expectation (under the null hypothesis of no group size differences among areas) are from area 3 (near the Galapagos Islands and South America), where there were more pods of 2 and 3+, and fewer single whales, than in the other areas.

DISCUSSION

Spatial patterns and habitat characteristics—All aggregations of blue whales identified here occurred in "upwelling-modified" waters, similar to the distribution of common dolphins, *Delphinus delphis,* in the ETP (Au and Perryman 1985). Baja California and Peruvian coastal waters form the low latitude terminations of very prominent eastern boundary current upwelling systems (Barber and Smith 1981). The Galapagos Islands are in the area of maximum intensity of equatorial upwelling, resulting from divergent flow of surface currents, island effects and the change in direction of Coriolis forces at the equator (Vinogradov

Table 1. Group size estimates for blue whales sighted in the eastern tropical Pacific, 1974–1988, by area: "1" is near Baja California (north of 15°N), "2" is off Central America near the Costa Rica Dome (4°N to 15°N), "3" is equatorial and off Peru and Ecuador (south of 4°N).

	Group size			
Area	1	2	3+	Total
1	32	4	7	43
2	103	29	18	150
3	6	7	5	18
Total	141	40	30	211

$\chi^2 = 13.52$, $P < 0.001$

1981). The origin of the Costa Rica Dome is a subject of debate (Hofmann *et al.* 1981, Wyrtki 1964), but it is a large (200-km diameter), quasi-stationary, counter-clockwise eddy. It occurs at the eastern and shallowest end of a zonal ridge in the thermocline extending along 10°N. Named for its upward bulging of the thermocline layer, the Dome is a site of active upwelling and nutrient enrichment of the surface layer (Owen 1981).

The most notable ecological attribute of upwelling-modified areas, which comprise blue whale habitat in the ETP, is relatively high primary and secondary productivity (Barber and Smith 1981, Vinogradov 1981, Owen 1981). The eastern boundary current upwellings off Baja California and South America are among the most productive areas of the world's oceans (Barber and Smith 1981). The equatorial and Costa Rica Dome upwellings are among the most productive parts of the pelagic ETP (Love 1972).

Euphausiids, the predominant prey of blue whales (Nemoto 1970), are the dominant form of crustacean micronekton throughout the region (Blackburn *et al.* 1970), and all of the areas occupied by blue whales there support relatively large standing stocks (Blackburn 1968). The distribution of blue whales in the ETP coincides closely with that of a group of four species of euphausiids: *Euphausia eximia, E. gibboides, Nematobrachion flexipes,* and *Nyctiphanes simplex* (Brinton 1979). Brinton (1979) termed this recurrent species group the "marginal proliferators" of ETP euphausiids, noting their great abundance in the region's upwelling areas. Sears (1987) and Gendron and Sears (1989) observed blue whales feeding on large concentrations of *N. simplex* on a number of occasions during spring months of 1984–1989 near Loretto and La Paz, inside the Gulf of California.

Whaling data indicate that blue whales rarely feed in low latitudes (Mackintosh 1966), but the habitats they occupy in the ETP indicate that feeding may be an important part of their low latitude life history. In fact, our data suggest that they select particular areas in the tropics most conducive to feeding success. It is quite possible that the empty stomachs recorded for whales outside of polar latitudes (mostly from land stations in temperate waters) were those of migrating whales, who fast during migration but engage in some foraging once they arrive at their "winter" areas.

Seasonal patterns—The April–June peak and July–September minimum in blue whale sightings recorded here along western Baja California are consistent with previously published information. The available data strongly suggest a fall migration south along the peninsula, into the Gulf of California (and perhaps farther south), followed by a spring migration north along the peninsula to the North Pacific. Rice (1974) reported a distinctly seasonal occurrence of blue whales off Baja California from both sightings and whaling records, with peak abundance from February through early July (when most were observed moving northward), and again in October (when most were observed moving southward), and no sightings from about November through January. Blue whales have been seen in the Gulf of California from January through August, but with peak presence in March–April (Sears *et al.* 1987; Vidal *et al.,* in press). The seasonal peak in blue whale occurrence along the Baja peninsula coincides with the spring and early summer peak in upwelling intensity and biological production (Bakun *et al.* 1974, Barber and Smith 1981).

Blue whales were recorded in all seasons off Central America. The Costa Rica Dome has likewise been observed in all seasons (Wyrtki 1964), always within about 200 km of 9°N, 89°W (Hofmann *et al.* 1981, Wyrtki 1964), even during the extreme 1982–1983 El Niño (Barberán *et al.* 1984). It is therefore one of the most predictable physical occurrences in the pelagic tropical Pacific. Studies of the biological oceanography of the Dome area disclosed no seasonal cycles, but rather a quasi-steady state in productivity and standing stocks from nutrients through micronekton (Blackburn 1966, King 1986), in contrast to the areas off Baja California and along the equator, which do undergo notable seasonal changes (Blackburn *et al.* 1970, Barber and Smith 1981). Gaskin (1982) concluded that the combination of high local productivity and considerable duration (as recorded for the Dome area) greatly favors the establishment of baleen whale populations.

It is difficult to make inferences about seasonality regarding the very few sightings made in this study near the Galapagos Islands and off Peru and Ecuador. We had limited sighting effort along the equator west of 100°W, and very little along the coast of Peru and Ecuador (Fig. 2), where previous studies indicate blue whales are relatively abundant (Donovan 1984, Clarke 1980). Sightings of blue whales made by whaling vessels operating out of Peru during 1976–1983 showed a seasonal peak during the southern summer (January–March), with a minimum during the southern winter and spring (May–December) (Donovan 1984).

Population identity—The blue whale sightings reported by Donovan (1984) and this study from equatorial waters and South American coast may represent the northernmost extension of the SE Pacific population, found along the South American coastal shelf and into the Antarctic (Mackintosh 1966). The cool water habitat they occupy extends up the coast to at least northern Peru and (seasonally) offshore along the equator with the extension of Peru Current into the South Equatorial Current (Wyrtki 1966). However, Donovan (1984) reported a southern summer peak in sightings off northern Peru, and noted this was inconsistent with the seasonal pattern expected for S. Hemisphere whales, which should be feeding then near Antarctica.

The blue whales sighted along western Baja California are almost certainly part of the NE Pacific population, which extends along the outer coast to at least northern California, with shore station captures reported from as far north as Vancouver Island (Kellogg 1929, Rice 1974, Scammon 1874). It is possible that this population also includes those blue whales sighted and captured in the Gulf of Alaska and near the Aleutian Islands (Nishiwaki 1966, Yochem and Leatherwood 1985).

It is difficult to connect the whales sighted near the Costa Rica Dome with either the NE or SE Pacific populations on the basis of present information. The Costa Rica Dome sighting aggregation is curiously present in all seasons, spatially separate from the other aggregations. There is no prominent stream of sightings between the Dome area and other areas (Fig. 1), as would be expected in an historical summary for a population that migrates seasonally.

Some hypotheses to explain the year-round presence and distinct spatial separation of the aggregation in the vicinity of the Costa Rica Dome are: (1) it consists of Northern Hemisphere animals in northern winter, Southern Hemisphere whales in southern winter (northern summer), coming and going via undetected routes; (2) it consists primarily of juveniles, not taking part in the full migration (as has been observed for other species of baleen whales: Gaskin 1982); (3) it is a resident, year round, distinct population. Berzin (1978) and Donovan (1984) both proposed that the blue whales off Central America could be part of a resident population that also included those whales seen off Peru.

The January–March density peak in relative abundance of blue whales near the Dome would imply that they are N. Hemisphere whales, but it is difficult to reconcile this connection with the distinct spatial gap between the Dome aggregation and the aggregation near Baja California. Given the rarity of blue whales, it is possible that N–S migrants from the area could escape notice, especially between the Dome aggregation and the equator. This is less likely to the north, where we have much more sighting effort, in all seasons. An inshore migration along the Mexican mainland is possible, but would likely have been observed by Mexican scientists studying baleen whales (O. Vidal, personal communication).

Taxonomic status—Since pygmy blue whales (*Balaenoptera musculus brevicauda* Ichihara 1966) were first described it has become evident that their distribution is much wider than originally thought (Berzin 1978). Donovan (1984) reported the likelihood that blue whales seen in equatorial and Peruvian coastal waters on the 1975 International Decade of Cetacean Research cruise were pygmy blues. This was based on observations of the Japanese whalers who made the sightings on the IDCR cruise and had seen both types in the Antarctic. However, Donovan (1984) and Ichihara (1981) stated that the two types could not be distinguished unequivocally in the water. Given this ambiguity, we attempted no subspecific designations of the sightings reported here. Likewise, we consider Berzin's (1978) designation of ETP blue whales as *B. m. brevicauda* to be premature, given the absence of morphometric or genetic data on blue whales from this region.

Concluding remarks—The primary reason for blue whales' migration to low latitudes is most likely related to thermal balance and calving success (*e.g.*, Lockyer and Brown 1981). However, we propose that foraging may be an important secondary factor. That is, once in low latitudes, blue whales select habitat which allows feeding.

The hypotheses discussed here regarding the population structure of ETP blue whales (including the possibility of a resident population), and the ecological processes underlying their occupation of upwelling-modified habitats, can be tested by a program of concentrated, contemporaneous sighting effort and oceanographic studies, and by photo-identification and/or biopsy-dart based genetic analyses. Photo matches or demonstration of genetic similarity between whales from the Costa Rica Dome and another area would be sufficient to indicate continuity. The sub-specific taxonomic status of ETP blue whales could also be addressed by such genetic analyses. Behavioral and oceanographic observations could address the following questions: are the whales feeding near the Dome? What species of euphausiids, if any, are aggregated in their immediate vicinity? Do they mate and/or calve there? Are the same individuals seen there year round?

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Literature Cited

Aguayo, A. L. 1974. Baleen whales off continental Chile. Pages 209–217 *in* W. E. Schevill, ed. The whale problem. Harvard University Press, Cambridge, MA.

Au, D. K. W., and W. L. Perryman. 1985. Dolphin habitats in the eastern tropical Pacific. Fishery Bulletin 83:623–643.

Bakun, A., D. R. McLain and P. V. Mayo. 1974. The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. Fishery Bulletin 72:843–844.

Barber, R. T., and R. L. Smith. 1981. Coastal upwelling ecosystems. Pages 31–68 *in* A. R. Longhurst, ed. Analysis of marine ecosystems. Academic Press, New York.

Barberán, J., A. Gallegos and A. R. Padilla. 1984. The Costa Rica Dome during the onset of the 1982–1983 El Niño. Tropical Ocean-Atmosphere Newsletter 24: 13–14.

BEKLEMESHEV, C. W. 1960. Southern atmospheric cyclones and whale feeding grounds of the Antarctic. Nature 187:530–531.

BERZIN, A. A. 1978. Whale distribution in tropical eastern Pacific waters. Report of the International Whaling Commission 28:173–177.

BLACKBURN, M. 1966. Relationships between standing crops at three successive trophic levels in the eastern tropical Pacific. Pacific Science 20:36–59.

BLACKBURN, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. Fishery Bulletin 67:71–115.

BLACKBURN, M., R. M. LAURS, R. W. OWEN AND B. ZEITZSCHEL. 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Marine Biology 7:14–31.

BRINTON, E. 1979. Parameters relating to the distributions of planktonic organisms, especially euphausiids, in the eastern tropical Pacific. Progress in Oceanography 8: 125–189.

CLARKE, R. 1980. Catches of sperm whales and whalebone whales in the southeast Pacific between 1908 and 1975. Report of the International Whaling Commission 30:285–288.

DONOVAN, G. P. 1984. Blue whales off Peru, December 1982, with special reference to pygmy blue whales. Report of the International Whaling Commission 34:473–476.

GASKIN, D. E. 1982. The ecology of whales and dolphins. Heinemann Educational Books, London and Exeter, NH.

GENDRON, D., AND R. SEARS. 1989. Relationship between blue whale and euphausiid concentrations in the southwestern Gulf of California during the 1984–1989 spring periods. Page 23 (Abstract), Proceedings of the Eighth Bienniel Conference on the Biology of Marine Mammals, Pacific Grove, CA.

HANSEN, D. V., AND A. HERMAN. 1988. A seasonal isotherm depth climatology for the eastern tropical Pacific. NOAA Technical Report ERL 434-AOML 33 (Revised).

HOFMANN, E., A. J. BUSALACCHI AND J. J. O'BRIEN. 1981. Wind generation of the Costa Rica Dome. Science 214:552–554.

HOLT, R. S., AND S. SEXTON. 1989. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1987 data. Report of the International Whaling Commission 39:347–351.

ICHIHARA, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda,* a new subspecies for the Antarctic. Pages 79–113 *in* K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley and Los Angeles.

ICHIHARA, T. 1981. Review of pygmy blue whale stock in the Antarctic. FAO Fish Series (5), Mammals in the seas 3:211–218.

KELLOGG, R. 1929. What is known of the migrations of some of the whalebone whales. Pages 467–494 *in* Annual Report Smithsonian Institution, 1928.

KING, F. D. 1986. The dependence of primary production in the mixed layer of the eastern tropical Pacific on the vertical transport of nitrate. Deep-Sea Research 33: 733–754.

LEATHERWOOD, S., AND R. R. REEVES. 1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco.

LOCKYER, C. H., AND S. G. BROWN. 1981. The migrations of whales. Pages 105–137 *in* D. J. Aidley, ed. Animal migration. Society for experimental biology seminar series 13. Cambridge University Press.

LONGHURST, A. R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Research 23:729–754.

LOVE, C. M. 1972. EASTROPAC atlas. Circular 330, National Marine Fisheries Service, Washington, DC, 3 volumes.

MACKINTOSH, N. A. 1965. The stocks of whales. Fishing News Books, London.

Mackintosh, N. A. 1966. The distribution of southern blue and fin whales. Pages 125–144 *in* K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley and Los Angeles.

Mitchell, E. 1975. Trophic relationships and competition for food in Northwest Atlantic whales. Pages 123–133 *in* Proceedings of the Canadian Society of Zoologists 1974.

Nasu, K. 1963. Oceanography and whaling ground in the subarctic region of the Pacific Ocean. Scientific Reports of the Whales Research Institute 17:105–155.

Nasu, K. 1966. Fishery oceanography study on the baleen whaling grounds. Scientific Reports of the Whales Research Institute 20:157–210.

Nemoto, T. 1957. Foods of baleen whales in the northern Pacific. Scientific Reports of the Whales Research Institute 12:33–90.

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. Scientific Reports of the Whales Research Institute 14:149–290.

Nemoto, T. 1970. Feeding pattern of baleen whales in the ocean. Pages 241–252 *in* J. H. Steele, ed. Marine food chains. Oliver and Boyd, Edinburgh.

Nishiwaki, M. 1966. Distribution and migration of the larger cetaceans in the North Pacific as shown by Japanese whaling results. Pages 170–191 *in* K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley and Los Angeles.

Owen, R. L. 1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects. Pages 197–233 *in* A. R. Longhurst, ed. Analysis of marine ecosystems. Academic Press, New York.

Polacheck, T. 1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tuna purse seiners. Ph.D. thesis, University of Oregon. 444 pp.

Rice, D. W. 1974. Whales and whale research in the eastern North Pacific. Pages 170–195 *in* W. E. Schevill, ed. The whale problem: a status report. Harvard University Press, Cambridge.

Scammon, C. M. 1874. The marine mammals of the northwestern coast of North America. John H. Carmany & Sons, San Francisco.

Sears, R. 1987. The photographic identification of individual blue whales (*Balaenoptera musculus*) in the Sea of Cortez. Cetus 7(1):14–17.

Sears, R., M. Berube and D. Gendron. 1987. A preliminary look at the distribution and migration of blue whales (*Balaenoptera musculus*) in the northeast Pacific, based on the photo-identification of individuals. Page 62 (Abstract), Proceedings of the Seventh Biennial Conference on the Biology of Marine Mammals, Miami, FL.

Uda, M. 1954. Studies on the relation between the whaling grounds and the hydrographic conditions (I). Scientific Reports of the Whales Research Institute 9:179–187.

Vidal, O., L. T. Findley, A. L. Figueroa, J. Maldonado, A. Robles and G. Carvallo. In press. Observaciones sobre la distribución, ciclo respiratorio y comportamiento de ballenas azules, *Balaenoptera musculus,* en El Golfo de California, México. *In* L. T. Findley and O. Vidal, eds. Memorias, XI Reunión Internacional sobre Mamíferos Marinos, 2–6 Abril 1985, Guaymas, Sonora, México.

Vinogradov, M. E. 1981. Ecosystems of equatorial upwellings. Pages 69–93 *in* A. R. Longhurst, ed. Analysis of marine ecosystems. Academic Press, New York.

Volkov, A. F., and I. F. Moroz. 1977. Oceanological conditions of the distribution of Cetacea in the eastern tropical part of the Pacific Ocean. Report of the International Whaling Commission 27:186–188.

Wade, L. S., and G. L. Friedrichsen. 1979. Recent sightings of the blue whale, *Balaenoptera musculus,* in the northeastern tropical Pacific. Fishery Bulletin 76:915–919.

Wyrtki, K. 1964. Upwelling in the Costa Rica Dome. Fishery Bulletin 63:355–372.

Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanography and Marine Biology Annual Review 4:33–68.

Yochem, P. K., and S. Leatherwood. 1985. Blue whale—*Balaenoptera musculus* (Linnaeus, 1758). Pages 193–240 *in* S. H. Ridgeway and R. Harrison, eds. Handbook of marine mammals, volume 3, The sirenians and baleen whales. Academic Press, London.

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Abstract.– Spiny lobsters *Panulirus marginatus* from the Hawaiian Archipelago have undergone heavy fishing pressure since 1980 and have experienced increases in asymptotic length and decreases in mean length at onset of egg production. Prior to the expansion of the fishery, allozyme variation was surveyed, and populations were found to be polymorphic at seven loci. In 1987 we collected spiny lobsters from two of the previously sampled locations (Necker Island and Maro Reef) to test for significant changes in population structure or level of genetic variability. No significant changes through time were found at five of the seven loci. Significant differences were detected at *Est3* and *EstD*; however, frequencies at esterase loci have been previously shown to fluctuate through time. Observed number of allelic classes and observed heterozygosities have remained unchanged. The data suggest that no change in the amount of variability has occurred in spiny lobster since the expansion of the fishery.

Genetic Variation in Highly Exploited Spiny Lobster *Panulirus marginatus* Populations from the Hawaiian Archipelago

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Commercial trapping for the spiny lobster *Panulirus marginatus* in the northwestern Hawaiian Islands began in 1976 shortly after research cruises documented the resource in abundance. Two banks, Necker Island and Maro Reef, have been most heavily fished since the beginning of the fishery. In 1986 and 1987 research cruises repeated the earlier sampling at Necker Island and Maro Reef by trapping at the same sites on each bank with the same gear to document any changes that had occurred in density, population, and genetic parameters (Polovina 1989). The repeat sampling documented substantially reduced lobster densities as indicated by catch rates, which in 1986–87 were 37% and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Polovina 1989). A statistically significant ($P<0.05$) increase in the asymptotic lengths and decreases in the mean lengths at onset of egg production occurred between the 1977 and 1986–87 sampling at both locations (Polovina 1989).

While changes in these population parameters could be due to density-dependence relationships, some type of genetic change also may have occurred from selection induced by the fishing pressure (Nelson and Soulé 1987). For example, the fishery harvests lobsters at about the size the females first begin producing eggs. It is estimated that spiny lobster enter the fishery at 3.1 years of age and that the mean age females begin producing eggs is 2.5 years (Polovina 1989). Thus, heavy fishing pressure may select for female lobsters that sexually mature at a smaller size. Reduction in the total amount of genetic diversity or changes in the stock structure of the exploited populations are also potential results of intense fishing pressure (Allendorf et al. 1987). These latter types of genetic changes can often be monitored through allozyme analyses (Nelson and Soulé 1987), and are the subject of this paper.

Spiny lobsters from seven localities in the Hawaiian Archipelago were collected between 1978 and 1980, prior to the expansion of the commercial fishery, and analyzed for allozyme variation by Shaklee and Samollow (1984). Although overall levels of variation were quite low, they observed polymorphism at 7 of the 46 loci examined. However, no clear pattern of genetic differentia-

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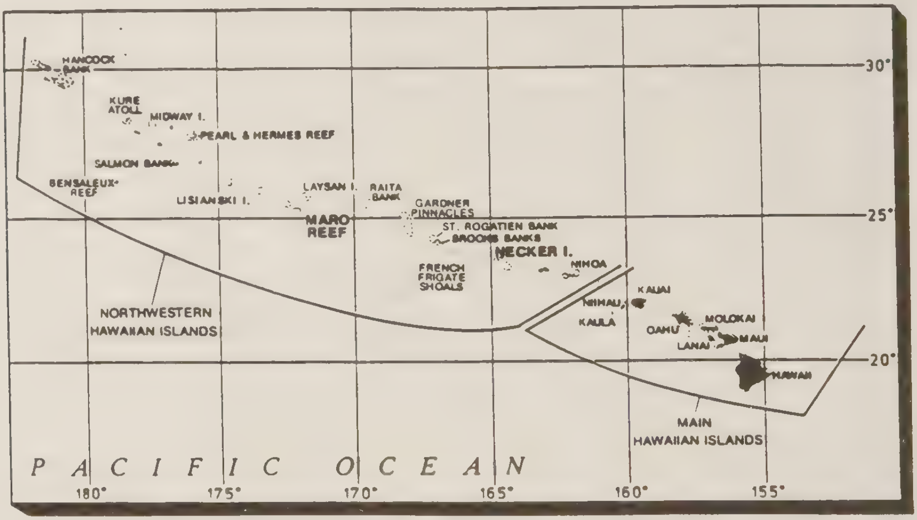
HANCOCK BANK
KURE ATOLL
MIDWAY I.
PEARL & HERMES REEF
SALMON BANK
BENSALEUX REEF
LISIANSKI I.
LAYSAN I.
RAITA BANK
MARO REEF
GARDNER PINNACLES
ST. ROGATIEN BANK
BROOKS BANKS
NECKER I.
FRENCH FRIGATE SHOALS
NIHOA
KAUAI
NIIHAU
KAULA
OAHU
MOLOKAI
LANAI
MAUI
HAWAII
NORTHWESTERN HAWAIIAN ISLANDS
MAIN HAWAIIAN ISLANDS
PACIFIC OCEAN
30°
25°
20°
180°
175°
170°
165°
160°
155°

Figure 1
Location of Maro Reef and Necker Island within the Hawaiian Archipelago.

tion among populations was detected, and they concluded that a single panmictic stock of spiny lobster exists throughout the Hawaiian Archipelago.

Our objective was to reexamine allozyme variation at those seven loci to determine if fishing pressure since 1980 affected population structure or genetic variability. During 1987, new collections of spiny lobsters from two of the same localities in the northwestern Hawaiian Islands (Maro Reef and Necker Island) were made. These two sites represent the mainstay of the commercial fishery. They are the most productive banks, have been fished the longest, and annually receive the greatest fishing pressure.

Analysis showed that the observed number of allelic classes and observed heterozygosity have remained essentially unchanged between 1978 and 1987. These data provide no evidence that population bottlenecks have occurred. Fishing pressure since 1980 has not reduced the genetic variability as detected by protein electrophoresis in spiny lobster from either of these two sites in the northwestern Hawaiian Islands.

Methods and materials

Muscle and digestive gland from 200 specimens from Maro Reef and Necker Island (Fig. 1) were collected, frozen onboard ship, and shipped frozen to the laboratory for analysis. Upon receipt, tissues were subsampled for electrophoresis and stored at −80°C for up to 4 weeks while analysis was completed.

Electrophoretic methods generally followed May et al. (1979) and Shaklee and Samollow (1984) to facilitate comparison. Samples were analyzed for the products of seven loci previously identified as polymorphic: *Est3*, Esterase, E.C. 3.1.1.–; *EstD* (*Umb*), Esterase, E.C. 3.1.–.–, resolved with 4-methylumbelliferyl acetate; *Gpi*, glucosephosphate-6-isomerase, E.C. 5.3.1.9; *Mpi*, mannose-6-phosphate isomerase, E.C. 5.3.1.8; *Pgm*, phosphoglucomutase, E.C. 5.4.4.2; *Tpep1,2* (*Pep-1,2*), tripeptidase aminopeptidase, E.C. 3.4.–.–, resolved with L-leucyl-L-leucyl-L-leucine. However, in contrast to the methods of Shaklee and Samollow (1984) who used horizontal and vertical gels, all analyses were performed on horizontal starch gels. *Tpep1* was resolved on an additional buffer, amine-citrate gel and tray buffer, pH 6.9 (Clayton and Tretiak 1972).

The electrophoretic data were analyzed using BIOSYS-1 (Swofford and Selander 1981). Allelic classes followed those of Shaklee and Samollow (1984), who pooled alleles into f(fast), m(medium), and s(slow) classes for numeric analyses. Pooling was required in their study and ours because many alleles were too rare to include in the statistical tests. Actual mobilities observed were also recorded.

Comparisons between the 1978–80 and 1987 data sets for each reef were performed using a chi-square contingency analysis based on the number observed in

Table 1

Allele frequencies for seven polymorphic loci in the spiny lobster *Panulirus marginatus*. Data from 1978–80 are those of Shaklee and Samollow (1984). Alleles are identified by relative mobility classes assigned by Shaklee and Samollow (1984). Actual mobilities observed in this study are also given. Numbers of individuals successfully scored are given in parenthesis.

	Est3			*EstD*			*Gpi*			
Location and date	f	m 100	s 93	f	m 100	s	f 100	m 88	s 66	ff 145
Maro Reef										
1978–80	0.003	0.957	0.040	0.001	0.988	0.010	0.959	0.039	0.002	–
		(386)			(340)			(320)		
1987	–	0.968	0.032	–	1.000	–	0.970	–	0.028	0.003
		(174)			(199)			(198)		
Necker Island										
1978–80	–	0.971	0.030	0.011	0.980	0.008	0.966	0.033	0.001	–
		(666)			(533)			(535)		
1987	–	0.992	0.008	–	1.000	–	0.955	0.002	0.020	0.022
		(194)			(200)			(200)		

	Mpi		*Pgm*			*Tpep1*		*Tpep2*		
	f 101	f+s 96, 100	f 200	m 100	s -33 -66	f 100	s 66	f •••	m 100	s 89
Maro Reef										
1978–80	0.011	0.989	0.007	0.984	0.009	0.725	0.275	–	0.988	0.012
	(418)			(345)		(142)			(335)	
1987	0.005	0.995	0.003	0.977	0.020	0.768	0.232	0.006	0.975	0.019
	(193)			(198)		(179)			(180)	
Necker Island										
1978–80	0.007	0.993	0.007	0.976	0.017	0.785	0.215	0.001	0.984	0.015
	(649)			(558)		(142)			(425)	
1987	0.003	0.998	–	0.985	0.014	0.768	0.232	–	0.980	0.020
	(188)			(200)		(144)			(176)	

each allelic class. Shaklee and Samollow (1984) found no heterogeneity between year classes for any loci except *EstD*, and thus they report pooled frequencies. They provide annual frequency estimates for *EstD* for 1979 and 1980.

We also compared the 1987 data sets from Maro Reef and Necker Island using chi-square contingency analysis.

Results

Allozyme analysis

All loci previously observed to be polymorphic were also found to be variable in the new samples, with the exception of *EstD* (Table 1). Allele classes observed by Shaklee and Samollow (1984) and not observed in this study were *Est3(f)*, *EstD(f)*, and *EstD(s)*. We observed *Gpi(145)* in both populations; this allele was not previously reported. Additionally, when analyzing *Tpep1* allozymes, we detected a *Tpep3(94)* allele in a single individual from Maro Reef which was not observed previously. Isozyme patterns agreed with descriptions provided in the earlier study. There were no indications of non-genetic variation at the esterase or any of the other loci.

Genotypic frequencies at all loci fit the expectation of Hardy-Weinberg equilibrium with the exception of *Est3* in Maro Reef ($P = 0.041$) and *Mpi* in both populations. *Mpi* has an unusual distribution of alleles between the two sexes (Shaklee 1983). Males always carry at least one slow allele, while females rarely have this variant. The common and slow variant alleles were pooled for the statistical analyses, and only the frequency of the fast allele is reported. With pooling, a test for fit to Hardy-Weinberg is possible, and no significant deviation from Hardy-Weinberg was observed.

Table 2

Average per locus and mean heterozygosity over all loci for spiny lobster *Panulirus marginatus* from Maro Reef and Necker Island.

Location and date	*Est3*	*EstD*	*Gpi*	*Mpi*[1]	*Pgm*	*Tpep1*	*Tpep2*	Mean[2]
Maro Reef 1987	0.061	0.000	0.059	0.381	0.045	0.356	0.049	0.021
Necker Island 1987	0.015	0.000	0.087	0.477	0.030	0.389	0.039	0.023
Hawaiian Archipelago 1978–80[3]	0.059	0.032	0.076	0.374	0.042	0.370	0.026	0.021

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[1] Sex restricted allele distribution (Shaklee 1983).

[2] 1987 estimate assumes monomorphism at the 39 additional loci surveyed by Shaklee and Samollow (1984).

[3] From Shaklee and Samollow (1984).

Chi-square analyses

Contingency chi-square analyses were performed between the two newly sampled collections at each of the polymorphic loci. Because of their low frequencies, all variant alleles at each locus were pooled into one class. Significant heterogeneity between Necker Island and Maro Reef was observed for *Est3* ($\chi^2 = 5.61$, df = 1, $P<0.020$).

Contingency chi-square analyses were also performed between the data gathered in this study and those of Shaklee and Samollow (1984) at each of the polymorphic loci. Significant heterogeneity was observed between the Necker Island 1987 and 1979–80 collections at *Est3* ($\chi^2 = 5.86$, df = 1, $P<0.025$).

Shaklee and Samollow (1984) reported fluctuating frequencies over years at the *EstD* locus and concluded that the 1980 samples represented a cohort with an unusual frequency. Therefore, we tested for heterogeneity between our data and the 1979 and 1980 *EstD* data separately. Both Maro Reef and Necker Island were significantly different for the 1980 comparison (Maro Reef, $\chi^2 = 9.71$, df = 1, $P<0.005$; Necker Island, $\chi^2 = 15.42$, df = 1, $P<0.001$). The Necker Island 1987 data were significantly different from the 1979 data ($\chi^2 = 6.10$, df = 1, $P<0.02$); the Maro Reef data were not significantly different.

Number of allelic classes

The total number of observed alleles at all sampled loci can also be used as an indicator of overall variability. Shaklee and Samollow (1984) observed a total of 18 different allelic classes in both the Maro Reef and Necker Island collections; we observed, for the same loci, 16 and 15 classes, respectively (Table 1). Although three classes (with frequencies of 0.010 or less) detected earlier were not observed in this study, two new alleles were observed.

It is also important to note the persistence of low-frequency allelic classes. *Gpi(s)*, *Pgm(f)*, and *Pgm(s)* were present in the 1978–80 Maro Reef collections at frequencies of 0.009 or less; all were present in the 1987 collection. *Gpi(s)* and *Mpi(f)* were present in the 1978–80 Necker Island collection at frequencies of 0.007 or less; both were present in the 1987 collection.

Heterozygosity

Heterozygosities were calculated for each locus for each population (Table 2). The *Est3* heterozygosities in the 1987 Necker Island collection were lower than those observed in the Hawaiian Archipelago during 1978–80 as no variants at this locus were observed. However, the 1987 Necker Island average heterozygosity over all loci was 0.023 (assuming monomorphism for the 39 additional loci previously resolved) compared with the value of 0.021 reported in the earlier study. Mean heterozygosities were statistically indistinguishable between the two populations and those observed in the earlier study. It should be noted, though, that differences on the order of 5% heterozygosities may require that large numbers of loci be screened to statistically test significant differences, and tests of heterozygosities are particularly insensitive when comparing low levels of heterozygosity such as observed in this study (Archie 1985).

Discussion

Stability of allele frequencies over at least 7 years was found at *Gpi*, *Mpi*, *Pgm*, *Tpep1*, and *Tpep2*. The gene frequencies of spiny lobster from Maro Reef and Necker Island appear to be stable both between collection sites and between years at all loci, with the exception of the two esterase loci. The variability at the two esterase loci is of particular concern. Is this variability indeed indicative of genetic isolation between the two sampling localities or of changes in the stock structure?

The data of Shaklee and Samollow (1984) showed that *EstD* allele frequencies fluctuate in spiny lobster. They detected annual significant fluctuations in allele frequency within localities, but these annual fluctuations were parallel among Maro Reef, Necker Island, and an additional locality, Kure Atoll. Thus, the fluctuating frequencies did not lead to any significant differences in allele frequency between localities within years.

Our data, 7 years later, are somewhat consistent with this pattern for *EstD*. We detected significant differences between years, but no significant differences were found between localities sampled the same year. These data support the contention that fluctuations in the northwestern Hawaiian Islands do occur in *EstD* allelic frequencies. The data are insufficient to warrant invoking selection or drift as an explanation; however, one suitable hypothesis might be that these fluctuations were caused by immigration of a closely related population differing only at *EstD* frequencies.

However, unlike the previous data set, our data show a significant difference between the 1987 Necker Island and Maro Reef collections at *Est3*. Such change at a single locus could indicate either selection or stochastic processes operating on the *Est3* allelic frequencies with a lack of gene flow between the two localities.

No significant differences in levels of heterozygosity were detectable. This finding is not surprising. The rate of change in heterozygosity based on random drift is inversely proportional to population size (Hartl and Clark 1989) and is calculated as

$$H_t = (1 - 1/2\,N)^t\, H_0$$

where H_0 is the original heterozygosity value, H_t is the heterozygosity value after t generations, and N is the population size. At most, four generations have passed since the previous sampling. Thus, heterozygosity values should be indistinguishable with population sizes characteristic of a commercially exploitable species.

An analysis of low-frequency or rare alleles is often a more sensitive test to detect changes in variability. We observed a number of low-frequency alleles that were previously detected by Shaklee and Samollow (1984). Gregorius (1980) estimates that a sample size of 754 or greater would be needed to assure a 95% probability of detecting all alleles at a locus with frequencies of 0.01 or greater. Sample sizes were large in the earlier study—ranging from 386 to 666—increasing the probability of detection of rare alleles. Thus, it was expected that some of the previously detected rare alleles would not be observed in the 1987 collections, where sample sizes were 200 or less. Our data suggest that there has been no overall reduction in number of rare alleles within the populations; in fact, we detected rare alleles that were previously undetected.

The unchanged average heterozygosities and the persistence of rare alleles indicate that there has been no measurable loss of genetic variability due to fishing pressure. An additional concern in the management of the lobster fishery is whether each bank is primarily a self-recruiting population with minimal larval recruitment coming from other banks, or whether larval recruitment at any bank comes from an archipelago-wide gyre so the depletion of the spawning stock at any one bank will not affect recruitment to that bank. The significant difference between the 1987 Necker Island and Maro Reef frequencies at *Est3* is consistent with the hypothesis that the banks are largely self-recruiting, although this locus also appears to have varied significantly over time. Additional genetic studies, possibly including more sensitive DNA markers, are warranted to further elucidate the amount of genetic differentiation between these two important lobster populations. At present, though, a conservative management strategy would be based on the existence of two self-recruiting populations rather than a strategy based on a single panmictic unit.

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Citations

Allendorf, F., N. Ryman, and F. Utter
1987 Genetics and fishery management: Past, present, and future. *In* Ryman, N., and F. Utter (eds.), Population genetics and fishery management, p. 1–19. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle.

Archie, J.W.
1985 Statistical analysis of heterozygosity data: Independent sample comparisons. Evolution 43:678–683.

Clayton, J.W., and D.N. Tretiak
1972 Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29:1169–1172.

Gregorius, H-R.
1980 The probability of losing an allele when diploid genotypes are sampled. Biometrics 36:643–652.

Hartl, D.L., and A.G. Clark
1989 Principles of population genetics, 2d ed. Sinauer Assoc., Inc., Sunderland, MA.

May, B., J.E. Wright, and M. Stoneking
1979 Joint segregation of biochemical loci in Salmonidae: Results from experiments with *Salvelinus* and review of the literature on other species. J. Fish. Res. Board Can. 36: 1114-1128.

Nelson, K., and M. Soulé
1987 Genetical conservation of exploited fishes. *In* Ryman, N., and F. Utter (eds.), Population genetics and fishery management, p. 345–368. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle.

Polovina, J.J.
1989 Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46:660–665.

Shaklee, J.B.
1983 Mannosephosphate isomerase in the Hawaiian spiny lobster *Panulirus marginatus*: A polymorphic, sex-linked locus useful in investigating embryonic and larval sex ratios. Mar. Biol. (Berl.) 73:193-201.

Shaklee, J.B., and P.B. Samollow
1984 Genetic variation and population structure in a spiny lobster, *Panulirus marginatus*, in the Hawaiian archipelago. Fish. Bull., U.S. 82:693-702.

Swofford, D.L., and R.G. Selander
1981 BIOSYS-1—a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281-283.

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ON THE MEASUREMENT OF ECONOMIC CAPACITY UTILIZATION FOR MULTI-PRODUCT INDUSTRIES*

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This paper considers capacity utilization measures for the multi-product firm. The single-product dual measure of capacity utilization easily extends to the multi-product case. Three possible extensions of the single-product primal measure are considered. Although each has its limitations because of the restrictions embodied in it, each provides different, yet potentially useful information about capacity utilization in a multi-product industry. The dual and primal measures of multi-product capacity utilization are applied to the multi-species New England fishing industry to evaluate the potential for capacity expansion under a regulatory program of license limitation.

1. Introduction

Measures of capacity utilization (CU) have been used for many years to analyze the current 'state' of the economy and the expansionary or contractionary forces that might exist. However, it is only recently that economists have attempted to develop CU measures that are closely tied to the economic theory of firm behavior. Pioneering studies in this area include the work by Klein (1960) and Hickman (1964), and more recently by Morrison (1985, 1986) and Berndt and Fuss (1986). These studies have defined CU using the concept of the firm's short-run cost function where one or more inputs are treated as quasi-fixed. Morrison (1985) proposes two alternative definitions, a primal measure defined in terms of the firm's output level and a dual measure defined in terms of the firm's costs.

To date, however, both the theoretical and the empirical development of these theory-based CU measures has been confined to the case of a single-product firm, i.e., a firm that produces a single output. In reality, many firms

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produce two or more outputs and thus should instead be viewed as multi-product firms. The growing body of literature devoted to developing a theory of the multi-product firm [Baumol, Panzar, and Willig (1982), Laitinen (1980), Lau (1978), Sakai (1974)] attests to their importance in empirical work. It would therefore be useful to have economic CU measures that can be applied to the case of a multi-product firm.

The purpose of this paper is to propose and illustrate empirically several alternative definitions of CU that are derived from the theory of the multi-product firm. We consider one dual measure and three alternative primal measures that differ in terms of the restrictions imposed. All of the measures can be viewed as generalizations of the single-product measures to the case of a multi-product firm.

The paper is organized as follows. We begin with a brief review of the single-product measures proposed by Morrison (1985) since these provide a point of departure for our analysis. The next section discusses a dual CU measure for the multi-product case. It is shown that the single-product dual measure can be easily extended to apply to the multi-product case. The extension of the single-product primal measure is more problematic because a scalar measure of output does not generally exist for multi-product firms. Section 4 considers three alternative generalizations. The first requires that the technology be homothetically separable in outputs, and is therefore applicable only to a subset of multi-product firms. The second does not require separability but assumes that all outputs change proportionately. It therefore can be thought of as a 'ray' CU measure. The final measure defines CU in terms of one of the outputs, holding the other outputs constant. Although this numerical CU measure will vary depending upon which output is used, we show that under fairly weak assumptions the conclusion about whether capacity is currently under- or overutilized will be unique.

The theoretical discussion of alternative CU measures is followed in section 5 by an empirical illustration. One industry that is characterized by multi-product production is the multi-species fishing industry, in which fishing vessels combine a vector of inputs (capital, labor, and fuel) to produce a vector of multiple products (different fish species). We use data from the New England otter trawl industry to illustrate an application of the use of our alternative measures with a translog variable cost function. This multi-product industry is not only one of the world's most valuable fishing industries, but as we discuss below, measures of capacity utilization can make an important contribution to regulatory programs designed to correct the market failure arising from an open-access resource.

2. Single-product measures

Consider a cost-minimizing firm that produces an output level $\bar{y}$ using n variable inputs $(x_1, \ldots, x_n)$ and one input (K) that is quasi-fixed, i.e., fixed in the short run but variable in the long run. Let the firm's variable cost function be given by $G(\bar{y}, w, K)$ where w is the vector of variable input prices. Short-run total costs $C = C(\bar{y}, w, K, P_K)$ are then $G + P_K K$, where P_K is the price of K. Given K, the capacity level y^* is defined to be the output level at which the short-run average cost ($SRAC$) curve is tangent to the long-run average cost ($LRAC$) curve. This can be found by differentiating C with respect to K and solving for $y^*(K, w, P_K)$, i.e., y^* solves

$$G_K(y, w, K) + P_K = 0. \tag{1}$$

Given this capacity output level y^*, the primal CU measure is then defined to be $CU_q \equiv \bar{y}/y^*$. If $CU_q > 1$, then $\bar{y} > y^*$ and there is pressure to increase investment in K. Likewise, $CU_q < 1$ implies disinvestment incentives. When $CU_q = 1$, K is the cost-minimizing level of capital for producing $\bar{y}$ and the firm has no incentive to change the level of K.

The primal CU measure captures the output gap that exists when actual output differs from capacity output. Alternatively, capacity utilization can be measured in terms of the cost gap that exists when $\bar{y}$ is not equal to y^*. If the firm were in long-run equilibrium, i.e., $\bar{y} = y^*$, then by (1), it must be true that

$$-G_K(\bar{y}, w, K) = P_K. \tag{2}$$

Since $-G_K(\bar{y}, w, K)$ can be interpreted as the shadow value of K (Z_K), this states that the firm is in long-run equilibrium if the shadow value of K is equal to the price of K. Thus, if $\bar{y}$ were the long-run capacity output level, the firm's cost would be given by the shadow cost

$$C^* = C(\bar{y}, w, K, Z_K) = G(\bar{y}, w, K) + Z_K K. \tag{3}$$

The cost gap that results from not being in long-run equilibrium then gives a dual CU measure, namely,

$$CU_c \equiv \frac{C^*}{C} = \frac{C(\bar{y}, w, K, Z_K)}{C(\bar{y}, w, K, P_K)} = 1 + \frac{(Z_K - P_K)K}{C}. \tag{4}$$

As before, $CU_c > 1$ implies $Z_K > P_K$ and investment incentives exist, while $CU_c < 1$ means $Z_K < P_K$ and the firm would like to disinvest.

3. Dual CU measures for multi-product firms

To extend the above CU measures to the multi-product firm let $\bar{y} = (\bar{y}_1, \ldots, \bar{y}_m)$ be an m-dimensional vector of output levels with m greater than or equal to one. Clearly $m = 1$ corresponds to the single-output case, and thus any CU measure derived for an arbitrary m could be used for the single-output firm. We can define the firm's variable cost function $G(\bar{y}, w, K)$ and short-run total cost function $C(\bar{y}, w, K, P_K) \equiv G(\bar{y}, w, K) + P_K K$ as before, where now y is a vector rather than a scalar. We will assume $\partial^2 C/\partial y_i \partial K \equiv G_{iK} \leq 0$, i.e., that an increase in K will not increase the short-run marginal cost of any output.[1]

Although a multi-product firm does not have a scalar measure of output, the cost of producing any vector of output is a scalar, and thus the dual measure of CU used for the single-product firm can also be used for the multi-product firm. More specifically, treating y as a vector in (1), we can still define the shadow value of the quasi-fixed input $Z_K = -G_K$ and the analogous shadow cost. The dual CU measure for the multi-product firm is then

$$CU_c \equiv \frac{C^*}{C} = \frac{G(\bar{y}_1, \ldots, \bar{y}_m, w, K) + Z_K K}{G(\bar{y}_1, \ldots, \bar{y}_m, w, K) + P_K K}$$

$$= 1 + \frac{(Z_K - P_K)K}{C(\bar{y}_1, \ldots, \bar{y}_m, w, K, P_K)}, \tag{5}$$

where (5) is a straight-forward extension of (4).[2] Thus, the single-product dual concept of CU carries over directly to the multi-product case.

4. Primal CU measures for multi-product firms

Unfortunately, the primal CU measure does not extend as readily. Because output is no longer a scalar, it is not possible to form the ratio of actual to capacity output to obtain a scalar CU measure. It is possible, however, to define analogous output-based measures of CU for the multi-product firm. In this section, we propose three alternative measures.

4.1. CU under homothetic separability

Suppose that the firm's technology is homothetically separable in outputs, i.e., the transformation function $F(y, x, K) = 0$ takes the form $\tilde{F}(h(y), x, K) = 0$ for some function h: $R^m \to R$, where h is homogeneous of degree one after normalization. This is essentially equivalent to assuming that the outputs can be aggregated into a single measure of aggregate output $h(y)$. Then the corresponding variable cost function will take the form

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[1] This assumption always holds at the cost-minimizing level of K if K is a normal input [Hof et al. (1985)]. However, it is not guaranteed to hold for all K. The results of Lau (1976) imply that the variable cost function G must be convex in (y, K). This only requires that $G_{ii}G_{KK} - G_{iK}^2 \geq 0$, where $G_{ii} \geq 0$ and $G_{KK} \geq 0$. It does not restrict the sign of G_{iK}. Furthermore, assuming K is a normal input is not sufficient to guarantee $G_{iK} \leq 0$ if $G_{ij} \neq 0$ for some j. Nonetheless, we maintain this assumption since it seems reasonable to assume that the firm operates in a region where the marginal cost of any output is a nonincreasing function of K.

[2] See Squires (1987b) for a discussion of a similar measure based on the restricted multi-product profit function.

$$G(y_1, \ldots, y_m, w, K) \equiv \tilde{G}(h(y), w, K), \tag{6}$$

for some function $\tilde{G}$: $R^3 \to R$ [Denny and Pinto (1978), McFadden (1978)].

Given any output vector $\bar{y}$, the long-run cost-minimizing level of K (K^*) can be found by differentiating total short-run costs $C = \tilde{G} + P_K K$ with respect to K and solving for K, i.e., $K^* = K^*(h(\bar{y}), w, P_K)$ solves

$$\tilde{G}_K(h(\bar{y}), w, K) + P_K = 0. \tag{7}$$

Although long-run and short-run average costs are not defined here as in the single-product case, K^* can still be interpreted as the value of K for which the long- and short-run total cost functions are tangent at $\bar{y}$.

Alternatively, (7) could be solved for $h(y)$ as a function of w, K, and P_K. We denote this solution $h^* = h^*(w, P_K, K)$. h^* can be interpreted as the value of aggregate output for which the long- and short-run cost functions are tangent given K. Thus, it is the multi-product analogue of y^* and CU_q can be generalized by using $h(\bar{y})$ and h^* instead of $\bar{y}$ and y^* in the definition. More specifically, we define a primal measure of capacity utilization under homothetic separability, CU_s, to be

$$CU_s \equiv h(\bar{y})/h^*. \tag{8}$$

Clearly, if $CU_s > 1$, i.e., $h(\bar{y}) > h^*$, then by (7) $-G_K > P_K$ and incentives for investment exist. Likewise, $CU_s < 1$ implies disinvestment incentives exist, while $CU_s = 1$ if the firm is in long-run equilibrium. Finally, if $m = 1$, then CU_s reduces to CU_q since h is proportional to y in this case.

4.2. A ray measure of CU

Since the assumption of homothetic separability is quite restrictive, it would be useful to provide a more general measure of multi-product CU. In the literature on multi-product firms it has often been convenient to define concepts assuming that all outputs increase or decrease in fixed proportions. For example, the concepts of ray average cost (RAC) and multi-product returns to scale are both based on this assumption [Baumol, Panzar, and Willig (1982)]. Although a profit-maximizing firm may not choose to change all outputs proportionately in response to a parameter change, the assumption of proportional changes in output is convenient, since it essentially converts the multi-product problem into a single-product one. In this subsection, we propose a CU measure based on the assumption that outputs move along a ray.[3]

We begin by writing the firm's short-run total cost function as

$$\hat{C}(\bar{y}, k, w, K, P_K) = G(k\bar{y}, w, K) + P_K K, \tag{9}$$

where $k > 0$ is a scalar. This gives the cost of producing any vector $k\bar{y} = (k\bar{y}_1, \ldots, k\bar{y}_m)$. $\tilde{C}(\bar{y}, 1, w, K, P_K)$ is then the total cost of producing the output vector $\bar{y}$, i.e., the firm's actual costs.

As before, long-run equilibrium requires that, for a given output vector $k\bar{y}$, K must be at its cost-minimizing level. Equivalently, it must be true that

$$G_K(k\bar{y}, w, K) + P_K = 0. \tag{10}$$

Eq. (10) can be solved for the cost-minimizing level of K, $K^*(k\bar{y}, w, P_K)$. Alternatively, treating K as fixed, we can solve (10) for k to get the optimal 'scale' of operation $k^*(\bar{y}, K, w, P_K)$. If $k^* > 1$, then to be in long-run equilibrium with the given level of K the firm would have to expand its level of operation, i.e., move out along the ray through $\bar{y}$. Equivalently, $k^* > 1$ implies that at the current output level $\bar{y}$ (corresponding to $k = 1$) $-G_K < P_K$ and incentives to disinvest exist.[4] Alternatively, $k^* < 1$ means that the firm would like to scale back its level of operation given K, or increase its level of K given its output levels.

This interpretation of k^* suggests a multi-product generalization of the primal measure CU_q based on the movement of all outputs along a ray. We propose the following measure:

$$CU_r \equiv 1/k^*. \tag{11}$$

This measure clearly sends the right 'signals' about the state of the economy since investment incentives exist when $CU_r > 1$ and disinvestment incentives exist when $CU_r < 1$. In addition, if $m = 1$, CU_r reduces to CU_q.

Finally, it should be noted that our definition of capacity utilization under homothetic output separability, CU_s, is a special case of the ray measure CU_r. This result can be seen in the following way. Suppose the technology is homothetically separable in outputs. Then $CU_s \equiv CU_r$ if and only if

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[3] It should be recognized from the start, however, that such a measure could be biased since it requires a firm's optimal expansion path to lie along a ray through the origin in output space so that all products are produced in fixed proportions. A firm may respond to exogenous shocks (e.g., changes in product prices) by altering its product mix, thereby producing along a different product ray. An analogous bias can exist in estimates of multi-product economies of scale [Bailey and Friedlaender (1982), Shaffer (1984)].

[4] This follows from the fact that G_K is a decreasing function of k as long as $G_{iK} \leq 0$ for all i and $G_{iK} < 0$ for some i.

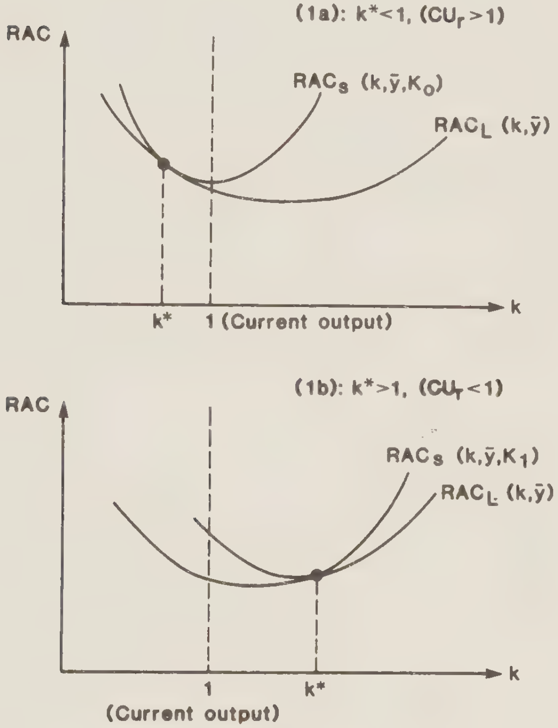

Fig. 1

$k^*h(\bar{y}) = h^*$. By the definitions of h^* and k^*, $-\tilde{G}_K(h^*, K, w) = P_K$ and $-\tilde{G}_K(h(k^*\bar{y}), K, w) = P_K$, which implies that $h^* = h(k^*\bar{y})$. Thus $CU_s \equiv CU_r$ if and only if $k^*h(\bar{y}) = h(k^*y)$, but this holds by linear homogeneity of h. The equivalence of the two measures is as expected since under homotheticity the expansion path for outputs is linear.

The ray measure of capacity utilization can be illustrated graphically using fig. 1. RAC_s is the firm's short-run ray average cost defined as $RAC_s \equiv C(k\bar{y}, K)/k$ (other arguments of C have been suppressed to simplify notation). It is drawn here as the familiar U-shaped curve. Likewise, RAC_L is the firm's long-run ray average cost defined by $RAC_L \equiv C(k\bar{y}, K^*(k\bar{y}))/k$ where $K^*(k\bar{y})$ is the solution to (10). Again, we allow it to be U-shaped. It reflects a cross-section of the firm's long-run total cost surface above the ray through $\bar{y}$. Note that the horizontal axis measures k rather than a scalar measure of output. Fig. 1a illustrates the case where the relationship between the level of K (here K_0) and the level of output $\bar{y}$ is such that capital is overutilized, i.e., $CU > 1$. If capital were at a different level, say K_1, capacity might be underutilized. This is illustrated in fig. 1b.

4.3. Partial CU measures

Both CU_s and CU_r as defined above allow all outputs to change in measuring the long-run equilibrium position of the firm. However, they impose restrictions on the technology (in the case of separability) or the way in which outputs can change (for the ray measure of CU). An alternative approach would vary only a single output in defining capacity output. This approach is discussed in this subsection.

Interpreting y in (1) as the vector $y=(y_1,\ldots,y_m)$, this equation can be solved for any given y_i in terms of the other $m-1$ output levels. In other words, if G_{iK} nonzero for all i, then (1) implicitly defines a set of explicit functions,

$$y_i^* = f_i(\bar{y}_{-i}, K, w, P_K), \qquad i=1,\ldots,m, \tag{12}$$

where $\bar{y}_{-i}$ denotes the $(m-1)$-dimensional vector $(\bar{y}_1,\ldots,\bar{y}_{i-1},\bar{y}_{i+1},\ldots,\bar{y}_m)$. We can then interpret y_i^* as the capacity level of output for the ith product given the actual output levels for all other products. A partial CU measure can then be defined as

$$CU_i \equiv \bar{y}_i/y_i^* \quad \text{for any given } i. \tag{13}$$

Of course, the numerical value of this CU measure will vary across products, and therefore it is not unique for a given firm. However, it can be shown that, if $G_{iK}<0$ for all i,[5] then these measures provide a consistent indication of whether the firm's capacity is currently under- or overutilized. We state this result in the form of a theorem.

Theorem 1. *If $G_{iK}<0$ for all i, then exactly one of the following holds:*

(i) $CU_i > 1$ *for all i,*
(ii) $CU_i < 1$ *for all i,*
(iii) $CU_i = 1$ *for all i.*

Proof. It is sufficient to show that under the above condition CU_i is greater than/ less than/ equal to one if and only if CU_j is greater than/ less than/ equal to one for all i and j; or equivalently, that $\bar{y}_i$ is greater than/ less than/ equal to y_i^* [defined in (12)] iff $\bar{y}_j$ is greater than/ equal to/ less than y_j^* for all i and j.

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[5] From the proof of the theorem, it is clear that this condition could be weakened to requiring that G_{iK} simply have the same sign for all i. However, assuming $G_{iK}>0$ for all i seems unreasonable.

Consider any two products i and j. Let $\bar{y}_{-ij}$ denote the $(m-2)$-dimensional vector of actual output levels excluding $\bar{y}_i$ and $\bar{y}_j$. We begin by noting that. since both $(y_i^*, \bar{y}_j, \bar{y}_{-ij})$ and $(\bar{y}_i, y_j^*, \bar{y}_{-ij})$ solve (1), and (12) is simply an explicit form of the implicit relationship in (1), it must be true that

$$y_i^* = f_i(\bar{y}_j, \bar{y}_{-ij}) \quad \text{and} \quad \bar{y}_i = f_i(y_j^*, \bar{y}_{-ij}). \tag{14}$$

Thus, to prove the theorem, it is sufficient to show that f_i is a strictly monotonically decreasing function of y_j. Implicitly differentiating (1) gives

$$\partial f_i/\partial y_j = \partial y_i^*/\partial y_j = -G_{Kj}/G_{Ki}, \tag{15}$$

which is negative if $G_{iK} < 0$ for all i. Thus f_i is strictly monotonically decreasing in y_j and the proof is complete. Q.E.D.

The intuition behind the theorem is the following. From (1) it is clear that, given the levels of all other outputs, if $\bar{y}_i$ is less than y_i^*, then $-G_K < P_K$ and there is an incentive to disinvest, i.e., capacity is underutilized. This is true regardless of which product we consider, i.e., which one we allow to adjust to equate the shadow value and the price of capital. Thus, the question of whether the firm faces expansionary or contractionary forces has the same answer regardless of which product is used to measure capacity utilization.

5. Empirical application

One industry where questions regarding capacity utilization have been raised is the fishing industry. Capital is generally measured in terms of vessel size (in gross registered tons), gear, and equipment. For any individual firm (often comprised of a single vessel) the level of capital can be viewed as quasi-fixed since in the short run vessel size cannot be easily varied. Measures of capacity utilization then provide an indication of whether the current level of capital is the long-run equilibrium level, and thus whether pressures for expansion or contraction of the industry exist.

In addition, measures of capacity utilization can provide an important contribution to designing regulatory programs which correct the market failure arising from the open-access nature of the resource. One of the most widely applied regulations, license limitation, restricts the number of vessels in the industry that can harvest the resource. As resource stocks recover and incomes eventually rise, fishermen invariably take advantage of any unused production potential or expand their capacity through additional investment to further increase their harvests and incomes. This, in turn, tends to drive the industry back to its original open-access condition. However, a multi-product CU measure calculated while planning for license limitation which includes vessel reductions would help adjust the number of vessels to both the resource conditions and each vessel's production capacity. Thus optimal utilization of both the resource stock and each individual vessel would be advanced. Participation could even be keyed by a vessel's extent of capacity utilization. Alternatively, if all vessels currently in the industry are grandfathered into the license limitation program, CU measurement would indicate if ancillary regulations are required to prevent full utilization of any unused production capacity or prevent further investment.

For these reasons, we choose a multi-product fishing industry to illustrate the proposed CU measures. The particular industry we consider is the New England otter trawl industry, which simultaneously harvests cod, flounder, haddock, redfish, pollock, and other species. An overview of the industry is provided by Squires (1987a).

To reduce the dimensionality of the problem, the many species harvested by the industry were aggregated (using Divisia indices) into three outputs: roundfish (cod and haddock), flatfish (flounders), and all others. These outputs are assumed to be produced (harvested) using two variable inputs, labor and fuel, and one quasi-fixed input, capital (represented by the vessel's gross registered tonnage).[6] The data set includes a cross-section of 42 vessels (firms) for 1980.[7] Outputs are endogenous and all firms are assumed to be profit maximizers.

The firm's variable cost function $G(y, w, K)$ is assumed to be of the translog form, which provides a second-order Taylor series approximation to an arbitrary variable cost function. Thus,

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[6] Capital is specified as quasi-fixed, because it is lumpy and difficult to adjust over short time periods. (Typically an existing vessel is sold and another one purchased and then overhauled and refitted or a new one is built.) Squires (1987b) applied Kulatilaka's (1985) test for full static equilibrium of capital with a profit function and found capital to be in full equilibrium. Yet, specifying capital as quasi-fixed in a cost function is nonetheless appropriate in this study, because translog profit and cost functions, when interpreted as approximations, are not self-dual. Moreover, when the observed levels of the quasi-fixed factor coincide with the desired levels, the restricted and full static equilibrium models are equivalent and either specification is appropriate.

[7] Squires (1987a) discusses the construction of the data in detail, including the firm-level prices for capital services. These were based upon vessel-acquisition prices (including hull, gear, equipment, and engine) obtained for vessels purchased in the period 1976 through 1979. Most of the prices were exact and compiled from bills-of-sale; the remainder were from federal tax returns. In most instances, information was available for additional gear and equipment purchased subsequent to the vessel's purchase. All values were deflated by the GNP implicit price deflator at the time of acquisition. Effects from capital vintage were assumed negligible during this period, since vessel and gear design remained constant. Both new and used vessels were included, although the majority were new vessels. All costs, output, and revenue data are confidential at the level of the individual firm.

The *ex ante* capital services price was derived from the capital stock acquisition price, and equals the sum of the depreciation and the opportunity cost of capital. Upon the recommendation of marine financial specialists, a 7% depreciation rate was applied. The opportunity cost of capital was assumed equal to Moody's long-term bond rate for utilities, which is 10.94% in 1980 and 15.72% in 1981. The *ex ante* capital services price (in $1972) ranged from $6,100 to $123,107 with a mean of $40,706 and standard deviation of $22,603.

$$\begin{aligned}\ln G = {} & A_0 + \sum_{i\in I} A_i \ln w_i + \sum_{j\in J} A_j \ln y_j + A_K \ln K \\ & + \tfrac{1}{2}\sum_{i\in I}\sum_{h\in I} A_{ih} \ln w_i \ln w_h + \tfrac{1}{2}\sum_{j\in J}\sum_{k\in J} A_{jk} \ln y_j \ln y_k \\ & + \tfrac{1}{2}A_{KK}(\ln K)^2 + \sum_{i\in I}\sum_{j\in J} A_{ij} \ln w_i \ln y_j \\ & + \sum_{i\in I} A_{iK} \ln w_i \ln K + \sum_{j\in J} A_{jK} \ln y_j \ln K, \qquad (16)\end{aligned}$$

where $I = \{L$ (labor), Z (fuel)$\}$ and $J = \{R$ (roundfish), F (flatfish), O (other)$\}$. The restricted share equations for the variable inputs are then obtained by Hotelling's Lemma:

$$\begin{aligned}S_i &= \partial \ln G/\partial \ln w_i \\ &= A_i + \sum_{h\in I} A_{ih} \ln w_h + \sum_{j\in J} A_{ij} \ln y_j + A_{iK} \ln K, \qquad (17)\end{aligned}$$

for $i = L, Z$. Finally, the assumption of profit maximization implies marginal-cost pricing for all of the outputs, i.e.,

$$p_j = \partial G/\partial y_j \quad \text{for} \quad j = R, F, O, \qquad (18)$$

where p_j is the price of output j. This implies that

$$\begin{aligned}S_j &= p_j y_j/G = \partial \ln G/\partial \ln y_j \\ &= A_j + \sum_{k\in J} A_{jk} \ln y_k + \sum_{i\in I} A_{ij} \ln w_i + A_{jK} \ln K, \qquad (19)\end{aligned}$$

for $j = R, F, O$. Eqs. (16), (17), and (19) were jointly estimated using the iterative Zellner estimator, with symmetry and linear homogeneity in prices imposed and with the fuel share equation dropped due to singularity.[8] The

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[8] An anonymous referee has noted that, under the assumption of profit maximization, output quantities are endogenous. Because outputs were specified as exogenously determined, a simultaneous equations problem arises. This issue will be addressed in future work by use of an instrumental variable estimator such as iterative three-stage least squares. Nonetheless, as brought to our attention by Arnold Zellner, the finite-sample properties of instrumental variable estimators are not entirely known, and thus there is no assurance that they will be better than those of our current estimates given our relatively small sample.

Table 1

Parameter estimates from translog variable cost function.[a]

Parameter	Estimate	Standard error
A_0	0.216	0.213
A_R	1.208	0.072
A_F	1.127	0.083
A_O	0.808	0.096
A_L	0.483	0.027
A_K	−0.362	0.297
A_{RR}	0.319	0.036
A_{RF}	0.020	0.032
A_{RO}	−0.056	0.030
A_{RL}	−0.014	0.011
A_{RK}	−0.003	0.106
A_{FF}	0.669	0.068
A_{FO}	−0.025	0.035
A_{FL}	−0.041	0.021
A_{FK}	−0.441	0.099
A_{OO}	0.076	0.032
A_{OL}	−0.030	0.011
A_{OK}	0.107	0.163
A_{LL}	0.166	0.153
A_{LK}	−0.090	0.030
A_{KK}	0.245	0.313

[a] All variables scaled by sample arithmetic mean.

resulting parameter estimates are reported in table 1.[9] The generalized R^2, which considers goodness of fit for the entire system of equations, is 0.999. This is computed as $1-\exp[2(L_0-L_1/N]$, where L_0 (L_1) is the sample maximum of log-likelihood when all slope coefficients are zero (unconstrained) and N is the sample size [Baxter and Cragg (1970)]. The R^2's for the ordinary least squares estimation of each individual equation are as follows:

Equation	R^2
$\ln G$	0.954
S_L	0.514
S_R	0.836
S_F	0.828
S_O	0.762

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[9] As a check on the soundness of these parameter estimates, the sign of the implied shadow price of capital was calculated. It was negative at the arithmetic sample mean and for 32 of the individual vessels. The 10 positive shadow prices of capital could reflect deterioration in performance of the second-order approximation when evaluated away from the point of approximation (the arithmetic sample mean in this case), which as noted by Wales (1977), can occur even if the data come from a well-behaved technology. Alternatively, the incorrect algebraic signs could reflect violations of correct model performance.

Table 2

Alternative capacity utilization measures.[a]

Dual measure:	CU_c	0.955	(0.045)
Ray measure:	CU_r	0.962	(0.052)
Partial measures:	CU_i for $i = R$	0.564	(0.102)
	$i = F$	0.714	(0.062)
	$i = O$	0.221	(0.237)

[a] Evaluated at arithmetic sample mean; linearized standard errors in parentheses.

The estimated parameters were used to calculate the dual, ray, and partial measures of capacity utilization. The CU measure under homothetic output separability was not calculated, since the data clearly rejected the separability hypothesis.[10]

The alternative CU measures are reported in table 2. Each is calculated at the arithmetic mean of the explanatory variables given in table 3. Linearized standard errors are given in parentheses.[11] All of the CU measures except for the third output's partial measure are statistically significant at 5%. Both the dual and ray CU measures suggest that in 1980 the New England otter trawl industry was very close to being in long-run equilibrium. This is consistent with Squires' (1987b) results using the test for long-run equilibrium suggested by Kulatilaka (1985). In interpreting CU_r, it should be remembered that this measure is subject to bias due to the maintained hypothesis that outputs are produced in fixed proportions (see footnote 3). Nonetheless, the fact that it provides results that are basically consistent with the dual CU measure and with previous work suggests that it may still be a useful indication of the current state of the industry.

The partial CU measures, the CU_i's, consistently indicate overcapitalization in the industry in 1980. Having partial CU measures that suggest overcapitalization is not necessarily inconsistent with the dual measure CU_c being close to one. Of course, $CU_c = 1$ implies $CU_i = 1$ for all i. However, if these measures converge at different rates (e.g., if costs are relatively insensitive to changes in output), then having short-run quantities that differ considerably

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[10] In addition, imposing homothetic (homogeneous) output separability on the translog variable cost function implies that variable costs are proportional to aggregate output $h(y)$, i.e., that there are short-run constant returns to scale in the production of aggregate output. This implies increasing returns to scale in the long run. However, this is not necessarily inconsistent with perfect competition, because as discussed by Baumol, Panzar, and Willig, multi-product industry structure depends not only upon the overall scale of production, but on cost economies arising from joint production and product diversity. Moreover, this seems to be a problem with the translog specification that would not exist with other flexible functional forms such as the normalized quadratic.

[11] The linearized standard errors were calculated, following the delta method, as first-order Taylor's series approximations [Efron (1981)]. Analytical derivatives were used for the linearized standard error of the dual measure. Numerical derivatives were used for the linearized standard errors of the ray and partial measures, where each parameter was altered by 0.1%.

Table 3
Sample statistics of explanatory variables ($1972).

w_L	$7837.67/person
w_Z	$0.574/gallon
w_K	$40,705.90/vessel
y_R	451,817 pounds
y_F	296,046 pounds
y_O	841,202 pounds
K	120.38 gross registered tons

from their long-run equilibrium levels will not necessarily imply having actual costs that differ considerably from shadow costs. In other words, output disequilibrium may not impose a very large cost penalty. Thus, the empirical results in table 2 seem to suggest that, in terms of its output levels, the New England otter trawl industry was overcapitalized in 1980, although this overcapitalization did not impose considerable costs on the industry.

Finally, the partial CU measures suggest that the degree of overcapitalization in the industry varied considerably across products. This highlights the importance of allowing for the multi-product nature of the industry in measuring capacity utilization. Treating the firm as a single-product firm (as is done implicitly in the calculation of the ray measure, CU_r) masks this variability. However, knowledge of the variability across products may have important implications for analyzing the expansionary or contractionary forces within an industry if these forces are product-specific. For example, based on our 1980 estimates for the otter trawl industry, there appears to be much more slack in the industry in its production of the residual ('other') category of fish than there is in its production of flatfish. Thus, the future demand for flatfish is likely to be of more importance in determining the future expansionary or contractionary forces in the industry than is the demand for the other types of fish.

A limited license program in the New England otter trawl industry would be able to match the number of vessels with the resource stock conditions without giving undue concern to expansion of production capacity and wasteful inputs ('capital stuffing') as the resource stock recovers and fishermen's incomes increase. Moreover, the partial CU measures suggest a supplementary production quota placed upon the flatfish species assemblage could help forestall the future expansions in fishing activity that plague license limitation.

6. Summary and conclusions

We have proposed several alternative measures of capacity utilization that could be used for a multi-product firm. Each is in some way an extension of the single-product measures that have been proposed elsewhere. The single-product dual measure of capacity utilization based on a comparison of actual and shadow costs extends easily to the multi-product case because it is a scalar regardless of the number of products produced. Extension of the single-product primal measure is more difficult. We have proposed three possible extensions. Although each has its limitations because of the restrictions embodied in it, each provides different yet potentially useful information about capacity utilization in a multi-product industry. Moreover, our application of these measures to the New England otter trawl industry highlights the importance of explicitly incorporating the multi-product nature of some industries into studies of capacity utilization.

References

Bailey, Elizabeth and Anne Friedlaender, 1972, Market structure of multiproduct industries, Journal of Economic Literature 20, 1024–1048.

Baumol, William, John Panzar, and Robert Willig, 1982, Contestable markets and the theory of industry structure (Harcourt, Brace & Jovanovich, San Diego, CA).

Baxter, N. and J. Cragg, 1970, Corporate choice among long-term financing instruments, Review of Economics and Statistics 52, 225–235.

Berndt, Ernst and Melvyn Fuss, 1986, Productivity measurement with adjustments for variations in capacity utilization and other forms of temporary equilibrium, Journal of Econometrics 33, 7–29.

Denny, Michael and Cheryl Pinto, 1978, An aggregate model with multi-product technologies, in: M.A. Fuss and D. McFadden, eds., Production economics: A dual approach to theory and applications (North-Holland, Amsterdam).

Efron, Bradley, 1981, Nonparametric standard errors and confidence intervals, Canadian Journal of Statistics 9, 139–172.

Hickman, Bert G., 1964, On a new method of capacity estimation, Journal of the American Statistical Association 59, 529–549.

Hof, John, Robert Lee, A. Dyer, and Brian Kent, 1985, An analysis of joint costs in a managed forest ecosystem, Journal of Environmental Economics and Management 12, 338–352.

Klein, Lawrence R., 1960, Some theoretical issues in the measurement of capacity, Econometrica 28, 272–286.

Kulatilaka, Nalin, 1985, Are observed technologies at long-run equilibrium? Tests on the validity of the static equilibrium model, Journal of Econometrics 25, 253–268.

Laitinen, Kenneth, 1980, A theory of the multiproduct firm (North-Holland, Amsterdam).

Lau, Lawrence, 1976, A characterization of the normalized restricted profit function, Journal of Economic Theory 12, 131–163.

Lau, Lawrence, 1978, Applications of profit functions, in: M.A. Fuss and D. McFadden, eds., Production economics: A dual approach to theory and applications (North-Holland, Amsterdam).

Morrison, Catherine, 1985, Primal and dual capacity utilization: An application to productivity measurement in the U.S. automobile industry, Journal of Business and Economic Statistics 3, 312–324.

Morrison, Catherine, 1986, Productivity measurement with non-static expectations and varying capacity utilization, Journal of Econometrics 33, 51–74.

Sakai, Y., 1974, Substitution and expansion effects in production theory: The case of joint production, Journal of Economic Theory 9, 255–274.

Shaffer, Sherrill, 1984, Scale economies in multiproduct firms, Bulletin of Economic Research 36, 51–58.

Squires, Dale, 1987a, Public regulation and the structure of production in multiproduct industries, Rand Journal of Economics 18, 232–247.

Squires, Dale, 1987b, Long-run profit functions for multiproduct firms, American Journal of Agricultural Economics 69, 558–569.

Wales, Terrence, 1977, On the flexibility of flexible functional forms: An empirical approach, Journal of Econometrics 5, 183–193.

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MONITORING INTERANNUAL CHANGES IN SPAWNING AREA OF PACIFIC SARDINE *(SARDINOPS SAGAX)*

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ABSTRACT

It is easier to monitor the spawning area of the Pacific sardine than to mount a full-scale effort to precisely estimate spawning biomass. Monitoring the spawning area may be particularly economical when the sardine is extremely rare or extremely abundant. Such imprecise estimates will probably not answer the management question of whether or not to set a specific biomass quota. The spawning area estimate is a candidate — with aerial surveys, scale sedimentation rates, and acoustic-trawl surveys — for use in interpolating between years when the more precise SWFC daily egg production method is used.

RESUMEN

Resulta más fácil monitorear el área de desove de la sardina del Pacífico que montar un estudio a gran escala que estime con precisión la biomasa del desove. El monitoreo del área del desove parece ser una salida económica cuando la abundancia de la sardina es extremadamente baja o extremadamente alta. Estas estimaciones imprecisas probablemente no contesten las preguntas administrativas relacionadas con la posibilidad de imponer una cuota a la biomasa específica. La estimación del área de desove junto con estudios aéreos, determinaciones de velocidad de sedimentación de las escamas, y estudios de arrastres acústicos sea probablemente el mejor método para interpolar datos entre aquellos años cuando el método mas preciso de la producción de huevos del SWFC es utilizado.

INTRODUCTION

The sardine fishery has been thoroughly reviewed by Ahlstrom and Radovich (1970). The fishery began in Monterey in the nineteenth century and grew to a maximum seasonal catch of just over 700,000 metric tons (MT) in the 1936–37 season. The catches began to disappear from the Pacific Northwest and northern California in 1945–46 and were inconsequential by 1952–53. There was a minor resurgence to 115,000 MT in the 1958–59 season; thereafter the fishery declined to very low levels.

There appears to be some recovery of the Pacific sardine stock (Parrish et al. 1989) off southern California (Wolf and Smith 1986; Wolf et al. 1987), as evidenced by the tendency for the spawning area to increase. Since 1986, small quotas for commercial catch have been permitted (907 MT for all use, 317 MT for live bait, 227 MT for dead bait). The incidental catch of sardine has also increased, particularly in the Pacific mackerel fishery (Wolf 1989). If the spawning biomass continues to increase, there will soon be a need for a management plan, and decisions will have to be made about monitoring the size of the stock. The moratorium on sardine catch for all uses was managed informally from 1974 to 1984 with an annual statement that the biomass appeared to be below 20,000 short tons. Currently, the spawning biomass of sardine is estimated from a spawning area relationship published by Wolf and Smith (1985). The quota of 907 MT for all uses has been constant since 1986, but may be increased by the California Department of Fish and Game.

The Southwest Fisheries Center Coastal Division has devised an absolute, instantaneous daily egg production method to estimate spawning biomass of northern anchovy (Lasker 1985). It remains for a management plan to determine how often and how precisely the spawning biomass of sardine must be monitored. Annual management advice is currently based on the stock synthesis model (Methot 1989; Lo and Methot 1989; Jacobson and Lo 1989).

Zweifel (1973) noted that the number of sardine eggs per positive station remained stable from 1951 to 1960, even as the population of sardine declined by nearly an order of magnitude. Smith and Richardson (1977: table 3.10) showed that the mean number of eggs per positive station varied little, even with different quantitative net tows and population sizes varying from 4 million to 200,000 tons. Wolf et al. (1987: table 2) demonstrated that the mean number per positive net tow remained stable, with a sardine spawning biomass estimated at 20,000 tons; thus, over a measured range of 20,000 to 4

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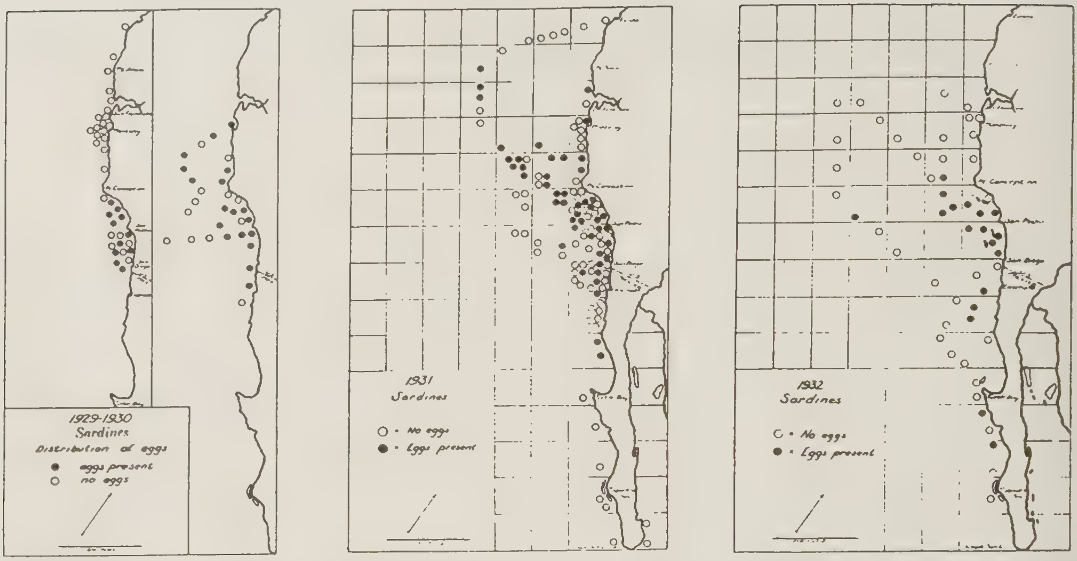

Figure 1. Locations of net tows taken to search for Pacific sardine eggs in April, May, and June 1929; April, May, and June 1930; February–August 1931; and February, April, and May 1932 (Scofield 1934). *Solid circles* indicate that the net tow was positive for eggs; *open circles* indicate that a net tow was taken and examined for eggs but none were found.

million tons of spawning biomass, the distribution of sardine eggs per positive station remains the same. We believe that this circumstance arises from the schooling habit of adults, regardless of the spawning biomass of the population; the further behavioral concentration of sperm and eggs by the fraction of fish involved in spawning at the time of external fertilization in the open sea; and the subsequent dispersal by turbulent diffusion (Smith 1973; Smith and Hewitt 1985; Mangel 1985; Mangel and Smith, in press). Theoretically, the number of eggs per positive station could decline at high biomass concentrations because filter feeding in schooling fishes like the sardine and anchovy may result in incidental cannibalism and predation of the eggs (Gulland 1971; Alheit 1987; Smith et al. 1990).

It is assumed that the management plan for sardine will be similar to that for anchovy, with two thresholds (PFMC 1983). When the spawning biomass is below the lower threshold, no fishery is permitted; when the spawning biomass is between the lower and upper threshold, a fixed fraction of the spawning biomass, based on demographic considerations, is established as a quota for the ensuing year; and when the spawning biomass is above the upper threshold, no further catch is authorized. The lower threshold is established at the point that the costs of the fisher's search for the remaining fish increase, and where further catches would probably delay the recovery of the stock to higher productivity. The upper threshold is established at the point where fleet and processor capitalization and costs of marketing would not be repaid owing to the temporary nature of high biomass. This requires rather precise monitoring of spawning biomass near the lower threshold, and less precise estimates at all other biomass levels. Also, the policy of using indices of abundance rather than annual absolute measures of abundance reduces management costs for assessing stock at higher levels of abundance while providing for a stable fishery.

It is the purpose of this paper to present data to aid in designing programs to estimate and monitor biomass. These programs should contribute to management of the Pacific sardine fishery and to the understanding of interactions among the sardines, other planktivorous fishes, and their environment. The data used in the original paper on this topic by Zweifel (1973) will be extended from 1940 to the present.

METHODS AND RESULTS

Surveys of sardine eggs and larvae were conducted in 1929–32 (Scofield 1934; figure 1), 1939–1941 (Ahlstrom 1948; Ahlstrom 1966; Smith 1972;

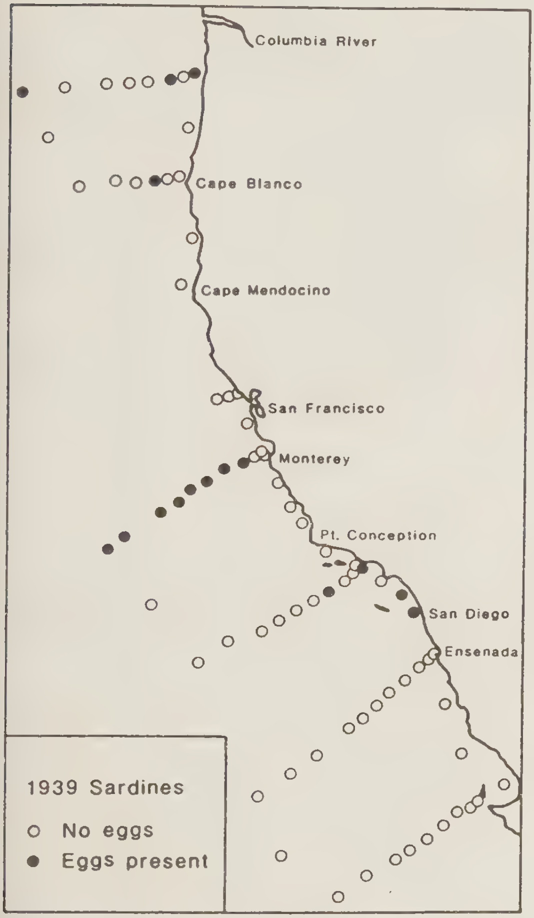

Figure 2. Locations of net tows taken to search for Pacific sardine eggs in May and June 1939 (Ahlstrom 1948). Net tows taken by Scofield (1934) were used to design the cruise.

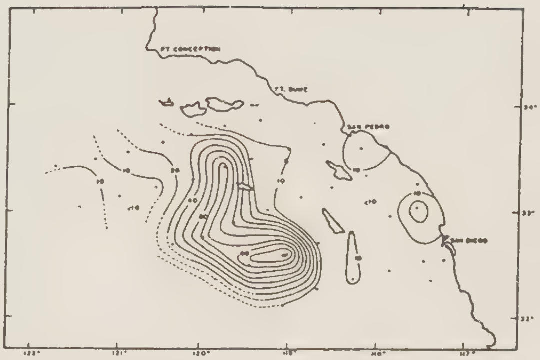

Figure 3. Contoured abundance of sardine eggs during the period of survey in 1941 (Sette and Ahlstrom 1948). These data are included in the analysis.

figure 2); and 1951–89 (CalCOFI on-line data system). Although distributions of eggs and larvae per net tow can be obtained for all these time periods, it is not possible to measure the areal boundaries of the spawning distribution for all sets of years. For this illustration, I have chosen the time series of sardine eggs and larvae for the area surveyed in 1941 (figure 3). At that time, virtual population estimates were based on the assumption that every female over 2 years old was a spawner; maturity and gonadal activity were not checked in each year.

The method used here for estimating biomass is the "index area" method. The quality of this method depends on the assumptions that the area chosen contains all the biomass, is a consistent fraction of the total spawning area, or contains a constant fraction of the spawning biomass. It is likely that all time series used will suffer from violation of the same assumptions, since all values contain measurement error, and the values are drawn from an autocorrelated time series. I do not believe the regression methods used (Williams 1983) are valid for direct estimates of spawning biomass for management purposes. Recognizing these limitations, I will use the well-known procedures for linear regression to evaluate the components of indirect measures of population size.

Regression Analysis

Data on egg and larval abundance are available for selected years for a major region of spawning. In a previous analysis of anchovy and sardine (Smith 1972), only the larval data were used. It was noted that larvae can be sampled over 3 weeks and disperse and cover more area than eggs, which can only be sampled over 3 days. In addition, the eggs retain the distributional characteristics of the schooled adults that spawned them. Although larvae have the statistical advantage of dispersal, over 3 weeks' time there may be considerably more variability in mortality than for eggs. In this study I use both egg and larval data as well as the biomass estimates from virtual population methods used for catch analysis from 1932 through 1965 (Murphy 1966: 1932–44; MacCall 1979: 1945–65; table 1). For the remainder of the text I use the notation as follows:

VPM—the biomass (MT) of sardines 2 years old and older;

E—the egg census estimate of abundance in the entire survey area (#/10m^2);

TABLE 1

Data for Regression Estimates Using the Census Estimate or the Partitioned Estimates of Eggs or Larvae and the Virtual Population Methods (*VPM*) for Pacific Sardine

Year	*N*	*E*	*L*	*PE*	*PL*	*VPM*
A. Years for which *VPM* is available						
1940	240	699.10	49.13	0.754	0.808	1759.6
1941	210	336.90	36.88	0.629	0.748	2457.1
1951	96	33.33	2.06	0.167	0.146	277.0
1952	152	6.85	3.49	0.099	0.105	136.0
1953	226	0.21	0.07	0.031	0.013	202.0
1954	219	39.67	11.98	0.146	0.110	239.0
1955	142	26.87	7.29	0.169	0.092	170.0
1956	156	47.88	6.90	0.090	0.045	108.0
1957	145	23.00	12.09	0.103	0.097	90.0
1958	171	86.38	8.86	0.298	0.310	177.0
1959	188	182.00	7.88	0.287	0.250	122.0
1960	197	117.14	4.47	0.183	0.168	88.0
1961	73	17.08	1.40	0.164	0.082	54.0
1962	64	1.77	0.95	0.016	0.047	27.0
1963	77	14.22	1.94	0.052	0.039	21.0
1964	183	0.43	0.00	0.022	0.005	11.0
1965	112	4.57	0.79	0.107	0.098	3.0
B. Years for which no *VPM* is available						
1966	169	2.01	0.29	0.012	0.053	
1969	147	0.33	0.26	0.027	0.041	
1972	118	0.00	0.03	0.000	0.008	
1975	267	2.54	0.07	0.026	0.007	
1978	189	0.38	0.18	0.026	0.016	
1981	139	0.99	0.23	0.029	0.007	
1984	141	3.40	6.50	0.064	0.043	
1985	99	10.96	8.80	0.061	0.051	
1986	183	3.45	3.62	0.011	0.044	
1987	81	18.73	23.00	0.062	0.111	
1988	85	40.75	2.25	0.082	0.047	
1989	72	61.00	4.96	0.111	0.167	

Key: *N* = number of net tows included; *E* = egg census estimate of abundance; *L* = larval census estimate; *PE* = proportion of net tows containing sardine eggs; *PL* = proportion of net tows containing sardine larvae; *VPM* = biomass of sardines 2 years old and older.

L—the larval census estimate (#/10m^2; Smith 1972);

PE—the proportion of the net tows containing sardine eggs (positive stations);

PL—the proportion of the net tows containing sardine larvae;

NE—the number of eggs per positive station (#/10m^2); and

NL—the number of larvae per positive station (#/10m^2).

NE and *NL* are not listed in table 1 because they are obtained simply by dividing the census estimate *(E)* by the proportion of positive stations *(PE)*.

Table 2 lists the parameters, the standard errors of estimate of the parameters, the Student's *t* value of the estimate, the probability of the *t* value, the *F* value of analysis of variance, and the probability of the *F* value. No constant is less than .05, thus all the equations were redone forcing the zero-intercept. Omission of the constant when evaluating *PE* did not materially change the *F* value of the analysis of variance.

Possibly the most significant result of this analysis for monitoring the sardine biomass is the weakness of number of eggs or larvae per positive station when coupled with the probability of a positive station; in both cases *p* is greater than .05 and negative in reflecting changes in biomass (*PE* and *NE*, *PL* and *NL* in table 2; see also *NE* in figure 4B). As in the previous analysis (Smith 1972), the constants are not important, and the larval time series, with or without inclusion of number per positive station (*NL*), are marginally better predictors of spawning biomass (actually biomass of age 2+) than the equivalent measures of eggs (table 2). This may simply reflect the longer duration and better mixing with resultant lower variance of the larval estimates. I use the proportion of eggs relationship (*PE*) to extend the biomass time series to the present (table 3; figure 4A).

Another significant result is that the standard errors of the parameter estimates are all relatively large. This implies than none of these estimates would be adequate for year-by-year management advice during close regulation of the fishery. It seems likely that some of this parameter error is due to the fixed maturation at 2 years of age. The largest deviations occur at the times of significant temperature anomalies. It may be that temperature plays an important role in determining the rate of maturation in sardine, as has been found for anchovy (Methot 1989). If the age at first maturity is shown to be influenced by temperature, it is likely that the VPA series could be adjusted from temperature records on hand (see Methot 1989, table 1).

Even with the improvement in accuracy, it does not appear from table 3 that useful estimates can be obtained from the level of sampling effort now being conducted in the quarterly CalCOFI surveys. Although the trend of recovery may be essentially correct, the spawning biomasses indicated may well be overestimates (Wolf and Smith 1986; Wolf et al. 1987). In the absence of an adequate SWFC daily egg production method estimate to provide a recent calibration, it does not seem likely that spawning area estimates alone will be adequate for setting quotas for the Pacific sardine fishery (figure 4A). The spawning area estimate would be useful for monitoring the sardine stock at high levels, and the area and VPM or stock synthesis estimates may be useful for examining this population's impact on the ecosystem. If the stock recovers to more than a million tons it may be necessary to conduct wide-ranging

TABLE 2

Comparison and Evaluation of Regression Parameters for Indirect Estimation of Spawning Biomass of Pacific Sardine

Predictor	Coef	SD	Student's *t*	*p*	*F*-ratio	*p*
A. With constant						
Constant	51.2	113.5	0.45	0 659	29.05	0.000
E	3.0976	0.5747	5.39	0.000		
Constant	−68.40	88.15	−0.78	0.450	68.12	0.000
L	45.489	5.511	8.25	0.000		
Constant	−225.5	108.7	−2.07	0.056	57.00	0.000
PE	2946.9	390.3	7.55	0.000		
Constant	−143.87	83.06	−1.73	0.104	88.96	0.000
PL	2651.7	281.1	9.43	0.000		
Constant	−77.5	214.0	−0.41	0.722	6.98	0.018
NE	1.4407	0.5453	2.64	0.018		
Constant	296.4	252.3	1.17	0.258	0.08	0.780
NL	1.114	3.921	0.28	0.780		
Constant	−85.78	91.08	−0.94	0.362	33.89	0.000
E	−1.034	1.188	−0.87	0.399		
L	58.22	15.64	3.72	0.002		
Constant	−158.8	115.2	−1.38	0.190	31.42	0.000
PE	3559.9	574.2	6.20	0.000		
NE	−0.6284	0.4432	−1.42	0.178		
Constant	−175.0	111.4	−1.57	0.139	42.17	0.000
PL	2647.8	289.2	9.16	0.000		
NL	0.669	1.536	0.44	0.670		
Constant	−67.0	113.2	−0.59	0.565	28.39	0.000
PE	−2425	2019	−1.20	0.253		
PL	5214	1669	3.12	0.009		
NE	−0.6225	0.3882	−1.60	0.135		
NL	2.183	1.519	1.44	0.176		
B. No constant						
E	3.2239	0.4891	6.59	0.000	43.44	0.000
L	43.032	4.455	9.66	0.000	93.30	0.000
PE	2379.4	305.9	7.78	0.000	60.52	0.000
PL	2345.1	231.6	10.12	0.000	102.50	0.000
NE	1.2915	0.3476	3.72	0.002	13.80	0.002
NL	4.527	2.663	1.70	0.109	2.89	0.109
E	−0.789	1.154	−0.68	0.505	45.33	0.000
L	52.27	14.26	3.67	0.002		
PE	3469.8	587.3	5.91	0.000	38.98	0.000
NE	−0.8776	0.4166	−2.11	0.052		
PL	2437.8	268.7	9.07	0.000	49.93	0.000
NL	−0.881	1.234	−0.71	0.486		
PE	−3963	1758	−1.69	0.116	39.12	0.000
PL	5620	1484	3.79	0.002		
NE	−0.6318	0.3781	−1.67	0.119		
NL	1.832	1.364	1.34	0.202		

Key: *E* = egg census estimate of abundance; *L* = larval census estimate; *PE* = proportion of net tows containing sardine eggs; *NE* = number of eggs per positive station; *PL* = proportion of net tows containing sardine larvae; *NL* = number of larvae per positive station.

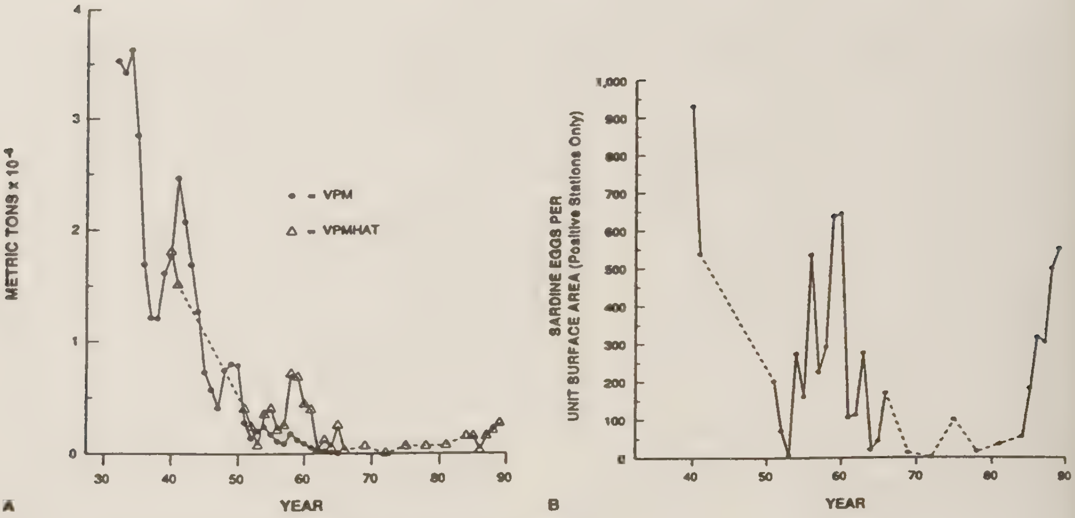

Figure 4. Time series plot of sardine 1932–89 (Murphy 1966: 1932–44; MacCall 1979: 1945–65). *A*, estimates using virtual population methods or egg incidence correlates (*PE*); *B*, estimated egg abundance per unit surface area at positive stations (*NE*).

surveys (figures 1 and 2) to accomplish a daily egg production estimate based on the extent of spawning in the 1929–32 and 1939 surveys (Scofield 1934; Ahlstrom 1948).

TABLE 3

Virtual Population Estimates of Sardine Spawning Biomass (2+) Derived from Regression on the Proportion of Positive Egg Stations in 1940–41 and 1951–65

Year	*N*	*PE*	VPMHAT
1940	240	0.754	1800
1941	210	0.629	1500
1951	96	0.167	400
1952	152	0.099	240
1953	226	0.031	74
1954	219	0.146	350
1955	142	0.169	400
1956	156	0.090	210
1957	145	0.103	250
1958	171	0.298	710
1959	188	0.287	680
1960	197	0.183	440
1961	73	0.164	390
1962	64	0.016	38
1963	77	0.052	120
1964	183	0.022	52
1965	112	0.107	250
1966	169	0.012	29
1969	147	0.027	64
1972	118	0.000	0
1975	267	0.026	62
1978	189	0.026	62
1981	139	0.029	69
1984	141	0.064	150
1985	99	0.061	150
1986	183	0.011	26
1987	81	0.062	150
1988	85	0.082	200
1989	72	0.111	260

Key: *N* = number of net tows; *PE* = proportion of net tows containing sardine eggs; VPMHAT = estimate of sardine biomass 2 years old and older based on the regression estimate of table 2, no constant.

DISCUSSION

Monitoring sardine biomass for fisheries management and ecosystem time series can be done with precise, but elaborate and expensive, egg production methods as used for the baseline studies of northern anchovy (Lasker 1985). Alternatively, indirect methods could be used, such as the deposition rate of scales (Soutar and Isaacs 1974) in anoxic sediments or traps; aerial surveys (Squire 1972); incidence and abundance of eggs or larvae; or trawl-acoustic methods in a mixed technique model (Methot 1989). Sardine stocks in the California Current region and other regions in the world fluctuate by orders of magnitude (Smith and Moser 1988; Lluch-Belda et al. 1989), and rough estimates of biomass may be sufficient for management plans during many periods of the species time sequence.

ACKNOWLEDGMENTS

I thank Patty Wolf, John Hunter, Izadore Barrett, Marc Mangel, Alec MacCall, and an unnamed reviewer for offering suggestions for materially improving the text. I am particularly grateful to Richard Charter and Cindy Meyer for maintaining the CalCOFI data base and writing special programs for extracting the data.

LITERATURE CITED

Ahlstrom, E. H. 1948. A record of pilchard eggs and larvae collected during surveys made in 1939 to 1941. Spec. Sci. Rep. U.S. Fish and Wildl. Serv. Fisheries (54), 82 pp.

———. 1966. Distribution and abundance of sardine and anchovy larvae in the California Current region off California and Baja California, 1951–64, a summary. Spec. Sci. Rep. U.S. Fish and Wildl. Serv. Fisheries (534), 71 pp.

Ahlstrom, E. H., and J. Radovich. 1970. Management of the Pacific sardine. *In* A century of fisheries in North America, N. G. Benson, ed. Special Publication No. 7, American Fisheries Society, Wash. D.C., pp. 183–193.

Alheit, J. 1987. Cannibalism versus egg predation: their significance in anchovies. *In* The Benguela and comparable ecosystems, A. I. L. Payne, J. A. Gulland, and K. H. Brink, eds. S. Afr. J. Mar. Sci. 5:467–470.

Gulland, J. A. 1971. Ecological aspects of fishery research. *In* Advances in ecological research, volume 7, J. B. Cragg, ed. New York: Academic Press, pp. 115–176.

Jacobson, L. D., and N. C. H. Lo. 1989. Spawning biomass of the northern anchovy in 1989. Southwest Fisheries Center Administrative Report LJ-89-17.

Lasker, R., ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA Tech. Rep. NMFS 36, 99 pp.

Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8:195–205.

Lo, N. C. H., and R. D. Methot. 1989. Spawning biomass of the northern anchovy in 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:18–31.

MacCall, A. D. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20:72–82.

Mangel, M. 1985. Search models in fisheries and agriculture. Lect. Notes Biomath. 61:105–138.

Mangel, M., and P. E. Smith. In press. Presence-absence sampling for fisheries management. Can. J. Fish. Aquat. Sci. 47.

Methot, R. D. 1989. Synthetic estimates of historical abundance and mortality for northern anchovy. *In* Mathematical analysis of fish stock dynamics, E. F. Edwards and B. A. Megrey, eds. Am. Fish. Soc. Symp. 6:66–82.

Murphy, G. I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. Fourth Series 34:(1)1–84.

Parrish, R. H., R. Serra, and W. S. Grant. 1989. Monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure, and zoogeography. Can. J. Fish. Aquat. Sci. 46:2019–2036.

PFMC: Pacific Fishery Management Council. 1983. Northern anchovy fishery management plan. PFMC, 526 S. W. Mill St., Portland, Oregon 97201.

Scofield, E. C. 1934 Early life history of the California sardine (*Sardina caerulea*), with special reference to distribution of eggs and larvae. Calif. Dep Fish Game Fish Bull. 41:1–48.

Sette, O. E., and E. H. Ahlstrom. 1948. Estimations of abundance of the eggs of Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. J. Mar. Res. 7:511–542.

Smith, P. E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. 70:849–874.

———. 1973. The mortality and dispersal of sardine eggs and larvae Rapp. P. -V Reun. Cons. Int. Explor. Mer 164:282–292.

Smith, P. E., and R. P. Hewitt. 1985. Anchovy egg dispersal and mortality as inferred from close-interval observations. Calif. Coop. Oceanic Fish. Invest. Rep. 26:97–110.

Smith, P. E., and H. G. Moser. 1988. CalCOFI time series: an overview of fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 29:66–78.

Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fisheries Tech. Pap. 175, FAO Rome, 100 pp.

Smith, P. E., H. Santander, and J. Alheit. 1990. Comparison of mortality rates of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, eggs off Peru. Fish. Bull. U.S. 87:497–508.

Soutar, A., and J. D. Isaacs. 1974. Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. Fish. Bull. U.S. 72:257–273.

Squire, J. L., Jr. 1972. Apparent abundance of some pelagic marine fishes off the southern and central California coast as surveyed by an airborne monitoring program. Fish. Bull. U.S. 70:1005–1019.

Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64:1283–1291.

Wolf, P. 1989. Review of some California fisheries for 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:7–17.

Wolf, P., and P. E. Smith. 1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 26:130–138.

——— 1986. The relative magnitude of the 1985 Pacific sardine spawning biomass off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:25–31.

Wolf, P., P. E. Smith, and C. L. Scannell. 1987. The relative magnitude of the 1986 Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 28:21–26.

Zweifel, J. R. 1973. A non-parametric approach to the estimation of relative change in fish population size from egg and larval surveys. Rapp. P. -V. Reun. Cons. Int. Explor. Mer 164:276–281.

9057

Leopard Shark *Triakis semifasciata* Distribution, Mortality Rate, Yield, and Stock Replenishment Estimates Based on a Tagging Study in San Francisco Bay

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Abstract.–Leopard shark tag recovery data, obtained from a 1979–88 study in San Francisco Bay, were analyzed to determine temporal and geographic distribution of the tagged population. Virtual population analysis of the tag recovery data was used to derive fishing mortality rates, which in turn were used to obtain yield-per-recruit and stock replacement values, and to estimate the effect of management by size limit on stock replenishment and yield per recruit.

Of the tagged population, 11% was recovered by sport anglers and commercial fishermen, and the distribution of recoveries indicates that leopard sharks are mostly resident in San Francisco Bay, although a portion of the population moves out of the Bay during fall and winter. An unusually high number of recaptures was made in 1983, a year of El Niño conditions and high river run-off. After obtaining mortality, yield, and stock replacement values, it was proposed that a viable management strategy for the San Francisco Bay leopard shark would be a size limit of 100 cm or 40 inches to ensure maintenance of the stock and provide a yield per recruit not too far below a maximum.

Shark has now become a familiar item at seafood counters and on restaurant menus in the United States (Slosser 1987), while in the past these fish were often discarded as trash fish, or at best valued for fish meal or their vitamin A-rich livers (Frey 1971). California has seen the rise of four new commercial elasmobranch fisheries since the mid-1970s (Holts 1988), and recreational shark fishing has grown in popularity in California and in other coastal states (Ristori 1987). The relatively rapid increase in shark harvesting has created a pressing need for more biological information to support management of targeted species, particularly information relating to population structure, mortality and replenishment rates, and degree of exchange between stocks. Elasmobranchs may be particularly vulnerable to exploitation, because they are generally slow growing and produce relatively few young, with recruitment appearing to be largely determined by parental stock size (Holden 1977).

The leopard shark *Triakis semifasciata* is harvested both commercially and recreationally in California. It occurs along the coast from Baja California, Mexico, to Oregon, and is very common in northern California bays (Squire and Smith 1977, Eschmeyer et al. 1983). Its fairly large size (maximum recorded is 180 cm; Kato et al. 1967) and accessibility in nearshore areas and bays probably contribute to its appeal with anglers and small-scale commercial boat operators. Reported commercial landings in California since 1980 have ranged from 18,199 kg (40,085 lbs) in 1980 to 45,994 kg (101,309 lbs) landed in 1983 (Table 1), with the San Francisco area contributing a large portion of the catch. Recreational landings are comparatively larger, judging from estimates of landings compiled by the U.S. Department of Commerce Pacific Coast Marine Recreational Fishery Statistics Survey (Table 2). Recorded commercial landings of leopard sharks may be misleading, as leopard sharks are often lumped with other species under the general category "shark, unspecified." Because of this reporting bias, it is difficult to determine the full extent of the commercial harvest. Further, it should be noted that reliable data for stratifica-

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Table 1

Reported commercial leopard shark landings (in kilos) by California port area. Source: Joyce Underhill, Calif. Dep. Fish Game, Long Beach, CA 90801, pers. commun., 17 May 1989.

Year	Eureka	San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	California total
1980	—	11 006	54	3 103	3 672	363	18 199
1981	94	12 334	55	5 505	3 482	1 913	23 384
1982	—	13 308	128	11 262	5 894	1 464	32 057
1983	—	33 764	202	7 218	2 632	2 177	45 994
1984	—	14 664	1 322	7 482	5 185	2 153	30 806
1985	24	8 054	7 620	8 135	8 725	1 871	34 430
1986	400	11 435	3 553	7 805	7 499	3 239	33 932
1987	741	6 684	3 523	6 357	6 113	1 720	25 138
1988*	1 263	2 367	2 038	5 161	3 728	4 357	18 914

*Preliminary.

Table 2

Reported commercial landings and estimates of the total marine recreational landings of leopard sharks in northern California, 1980–87. Recreational landings are Type A catches (observed landings) for north of San Luis Obispo County to the Oregon border, based on the Pacific Coast Marine Recreational Fishery Statistics Survey (provided by John F. Witzig, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Silver Spring, MD 20910, 14 June 1989). Commercial landings are summed for northern California ports.

	Northern California landings	
	Commercial	Recreational
Year	(kilos)	(kilos)
1980	11 060	68 682
1981	12 484	62 664
1982	13 436	7 578
1983	33 966	116 517
1984	15 986	33 610
1985	15 698	131 787
1986	15 388	158 778
1987	10 948	289 097

tion of catch and effort by moderately small time or area segments are unavailable for either the recreational or commercial fisheries. The smallest divisions for the recreational fishery are northern and southern California. For the commercial fishery, only the place of landing and not the place of catch is recorded, and effort data are nonexistent.

Information on reproduction, stock replacement rates, and stock interaction is scanty and mostly undocumented. Estimates of length at maturity for males have ranged from 70 to 119 cm and for females from 100 to 129 cm; size at birth is about 20 cm (Ackerman 1971, Compagno 1984, Kusher 1987). The gestation period is estimated at 10–12 months and parturition takes place in spring, according to Ackerman (1971) who worked with Elkhorn Slough fish in Monterey County, California. Certain other observations corroborate this. Moser and Sakanari* examined an aggregate of pooled embryos from fish taken in the fall in San Francisco Bay and the measurements formed a unimodal distribution with little variation in embryo sizes among litters, which is the expected pattern for an annual reproductive cycle. More than one mode among litters would be observed for a gestation period of 2 or more years. In addition, R. Russo (East Bay Park Dist., Alameda, CA 94169, pers. commun., 27 March 1984), sampling in South San Francisco Bay, has noted a predominance of pregnant females with near-term pups mainly from March through June (April–May peak), indicating a once-a-year parturition in spring. Pupping could be annual and occur in alternate years, with a 'recuperative' year between, but then about half of the mature female population would be in a nonreproductive condition at any given time. Of the 90 females over 120 cm that Ackerman (1971) examined from Elkhorn Slough, 94% had embryos or fertilized eggs in at least one ovisac; and all females >110 cm total length (TL) collected by Kusher (1987) in Elkhorn Slough and Monterey Bay and San Francisco Bay showed signs of either pregnancy, recent birth, or embryo abortion. Therefore, we use the assumption of an annual reproductive cycle in later sections dealing with stock replacement by reproduction. The leopard shark is primarily a benthic feeder (Russo 1975, Talent

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*Drs. M. Moser and J. Sakanari (Long Marine Lab., Univ. Calif., Santa Cruz, pers. commun., Sept. 1984) report that in a sample of nine pregnant females taken on 10 September 1984, presumably in midterm, the mean embryo length was 11.26 cm (1.51 SD), ($n = 51$ embryos).

1976). Prior to the work described here, nothing was known of its movements or the degree of exchange with other leopard shark populations along the California coast.

In 1979, a tagging study was initiated in San Francisco Bay to obtain information on age validation, growth, and movements of this species. Tag recaptures were monitored over a 9-year period. This report gives results of movements that were deduced from the temporal and geographic distribution of tag recoveries. In addition, although beyond the planned design of this study, we decided to utilize the tag recovery data together with published information to estimate the effect of management by size limit on stock replenishment and on yield per recruit. The lack of suitable statistical information on catches, as mentioned previously, prevented us from performing analyses that involve weighting tag recoveries by catch or effort. Results of the age validation segment of the study have been published elsewhere (Smith 1984), and results on age and growth are also being published separately (Kusher et al. In prep.).

Methods

All sharks were tagged off Hunters Point in south San Francisco Bay in 1979. Collections were made with a 183-m longline rigged with an average of 150 baited hooks fished on the bottom at depths of 15–20 m. Prior to release, total and precaudal lengths were recorded to the nearest centimeter, and each fish was given an intraperitoneal injection of oxytetracycline hydrochloride to mark vertebral centra for age verification purposes (Smith 1984). A record was made of the sex and general physical condition of each fish; seriously injured animals were not tagged. Those with minor hook injuries or with partially everted stomachs were classified as "injured"; the rest were classified as "healthy." A plastic rototag of the type recommended by Kato and Carvallo (1967) was applied to the first dorsal fin and the fish released at the capture point. The fin tags were imprinted with a legend informing the recoverer that a reward (amount unspecified) was offered for return of the tag and the fish or a section of its vertebral column for age verification purposes. The legend also provided an address and phone number to contact to arrange delivery.

Mortality estimation

Fishing mortality rates were estimated from the tagging data using the concept described by Murphy (1965), Gulland (1965), and Tomlinson (1970), which is now commonly referred to as virtual population analysis (VPA), though it differs from the original VPA procedure of Fry (1949). The computer program COHORT, written by John Geibel and Phil Law (Calif. Dep. Fish Game, 411 Burgess Drive, Menlo Park, CA 94025) was used to calculate the estimates. The natural mortality estimate was based on Hoenig's (1983) regression equation $\log(Z) = 1.46 - 1.01 \log(t_{max})$ where Z is the instantaneous annual total mortality coefficient and t_{max} is maximum age attained by the species. If the maximum age was determined from a period when there was virtually no fishing directed at the species, then one could assume the estimated Z approximates the instantaneous annual natural mortality coefficient, M.

The basic procedure involved assuming values of M over each 1-year time interval, taking a trial value of F_n, the instantaneous annual fishing mortality coefficient, for the ultimate interval, and executing the backward VPA computation on the tag recoveries to obtain an estimate of N_0, the number of tagged fish at the beginning of the first interval. Trial values were then iterated until the series converged on N_0.

Before conducting the VPA, it was necessary to consider two additional factors which would cause adjustments to the actual observations used in the analysis: (1) the likely rate of tag loss and (2) the level of tag recovery nonreporting. Since the tagging experiment was not designed for this type of analysis, there were no built-in procedures to estimate these factors. We therefore used what we judged to be the best available information from outside sources.

Yield per recruit

Yield per recruit was calculated by piecewise integration of the yield curve. The yield in weight at each age was taken to be the product of the annual rate of exploitation, the midpoint between an individual's weights at the beginning and end of the age interval, and the population size at the beginning of the interval.

$$Y = \exp[-M(t_{r'} + 1)]\,[1 - \exp(-Z)]\,(F/Z)$$

$$\times \sum_{t \geqslant t_{r'}}^{t_{max}} \{\exp[-Z(t - t_{r'})]\}\tilde{w}_t \qquad (1)$$

where Y is yield per recruit in weight (kg), t is age, $t_{r'}$ is age at first capture, and $\tilde{w}_t$ is the midpoint between the weights at t and $t + 1$.

Weight at age was computed by using predicted values from the von Bertalanffy length equation from Kusher (1987) and the weight-length formula in Smith (1984). Note that equation (1) assumes constant M and Z except that natural mortality is doubled during

Figure 1

Map of San Francisco Bay showing location of release area (arrow) and major Bay Area divisions and names referred to in the text.

year 1. This gives some weight to a higher mortality these young fish must suffer relative to the adult sharks. The phenomenon of the young being preyed on by larger sharks has been cited by Springer (1960, 1967) and by Holden (1974).

Stock replacement

Also calculated for various levels of age at first capture (knife-edge selection) and fishing mortality were the percentages of stock which would be replaced due to reproduction. Assuming an even division among the sexes, this was done by summing over ages, from age at first maturity to maximum age, the products of the number of female survivors per recruit and the number of pups produced by females at each age above the age of maturity and multiplying this sum by 100. For given $t_{r'}$ and F

$$R = \sum_{t \geq t_m} 50 \exp[-M(t+1) - F(t - t_{r'})\,\delta]\, P_t \qquad (2)$$

where t_m is female age at maturity, R is stock replacement per recruit in percent, P_t is estimated number of progeny produced annually by an age t female, and

$$\delta = \begin{cases} 1 & t > t_{r'} \\ 0 & t \leq t_{r'} \end{cases} \qquad (3)$$

Fecundity as a function of maternal body weight was estimated by fitting a monomolecular curve of the form $P_t = \beta - \theta \rho^{w(t)}$, with P the number of progeny, $w(t)$ the weight of the female at age t, and β, θ, and ρ constants. For computation, age at maturity was taken as the age corresponding to the weight which produced a value of zero for P_t in the above equation.

Ackerman (1971, his table 6) gives the numbers of embryos observed in 66 female leopard sharks ranging in size from 9.3 to 16.3 kg. Although his data are in a form which allows only the computation of mean number of embryos per female for five weight classes, he does give the number of females observed in each weight category. Using the numbers of females as weighting factors, the curve was fitted to these means with the Levenberg-Marquardt algorithm as implemented in the NCSS nonlinear regression program*.

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*Number Cruncher Statistical System, Version 5.3–Power Pack, 1988. NCSS, Kaysville, UT 84037. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Progeny as a function of maternal age was then estimated by applying the weight-length-age relationships cited above. We assume all nondeformed embryos survive to time of birth. Data were not available for applying the preferable procedure of directly regressing fecundity on age.

Geographical names and location of the tagged-fish release area are given in Figure 1.

Results

Tagging

A total of 948 sharks were tagged off Hunters Point, San Francisco, in south San Francisco Bay between 26 July and 13 September 1979. Most were tagged in August (68%) and September (26%). The hook rate was very high: 22 *Triakis* per 100 hooks, and a 44% hook rate for all elasmobranchs. Other sharks and rays taken in order of abundance were brown smoothhound *Mustelus henlei* ($n = 872$), bat ray *Myliobatis californica* ($n = 159$), soupfin shark *Galeorhinus galeus* ($n = 6$), sevengill shark *Notorhynchus cepedianus* ($n = 5$), and spiny dogfish *Squalus acanthias* ($n = 2$).

The lengths of tagged leopard sharks ranged from 51 to 144 cm TL (mean 81 cm, Fig. 2). The male:female ratio was 53:47. Large individuals may have been underrepresented in the tagging, since only 9% of females and 11% of males were over 100 cm. Commercial fishermen have reported a higher proportion of large fish in their catches, fishing at the same time with similar gear but in different areas of the south bay (B. Van Gorp and B. Fraser, commercial shark fishermen, pers. commun., June 1980). On the other hand, leopard sharks were probably recruited to our gear at a larger size than would be true for typical sportfishing tackle. Anglers fishing from shore and piers using small hooks would surely take a higher percentage of fish under 70 cm than that shown in Figure 2.

Of the 948 fish tagged, 82 individuals were classified as "injured" and the remaining 866 fish as "healthy." Return rates would presumably be higher for healthy, uninjured fish than for injured fish if the tagging operation caused mortalities; the absence of such a difference could be taken as suggestive of little or no tagging-induced mortality (Gulland 1983).

Recoveries

As of 30 September 1988, 108 fish had been recaptured of which 101 had known recapture date and location. A breakdown of all methods of recapture is given in Table 3, and provides an interesting glimpse of the various users of the leopard shark resource. The proportions reported by each group should approximate the proportions of the natural population harvested or caught by each group.

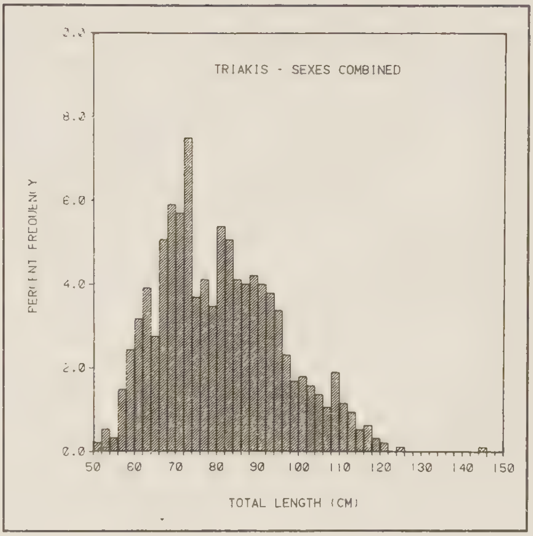

Figure 2
Length frequency of tagged leopard sharks (sexes combined) released off Hunter's Point in south San Francisco Bay, California, 1979.

Table 3
Distribution of leopard shark tag recaptures by recovery method and area in and around San Francisco Bay, California, 1979–88.

	Area of recapture			
Method of recapture	South bay	Central & north bays	Outside bay/ ocean	Totals
Recreational				
Private boat/skiff	32	15	1	48
Sportfishing boat (commercially operated)	0	4	0	4
Bank	13	3	2	18
Pier	10	6	0	16
Jetty	0	1	0	1
Bridge	1	0	0	1
Total	56	29	3	88
Commercial				
Bottom trawl	0	0	5	5
Gillnet	0	0	4	4
Longline	4	0	0	4
Total	4	0	9	13
Total all methods	60	29	12	101

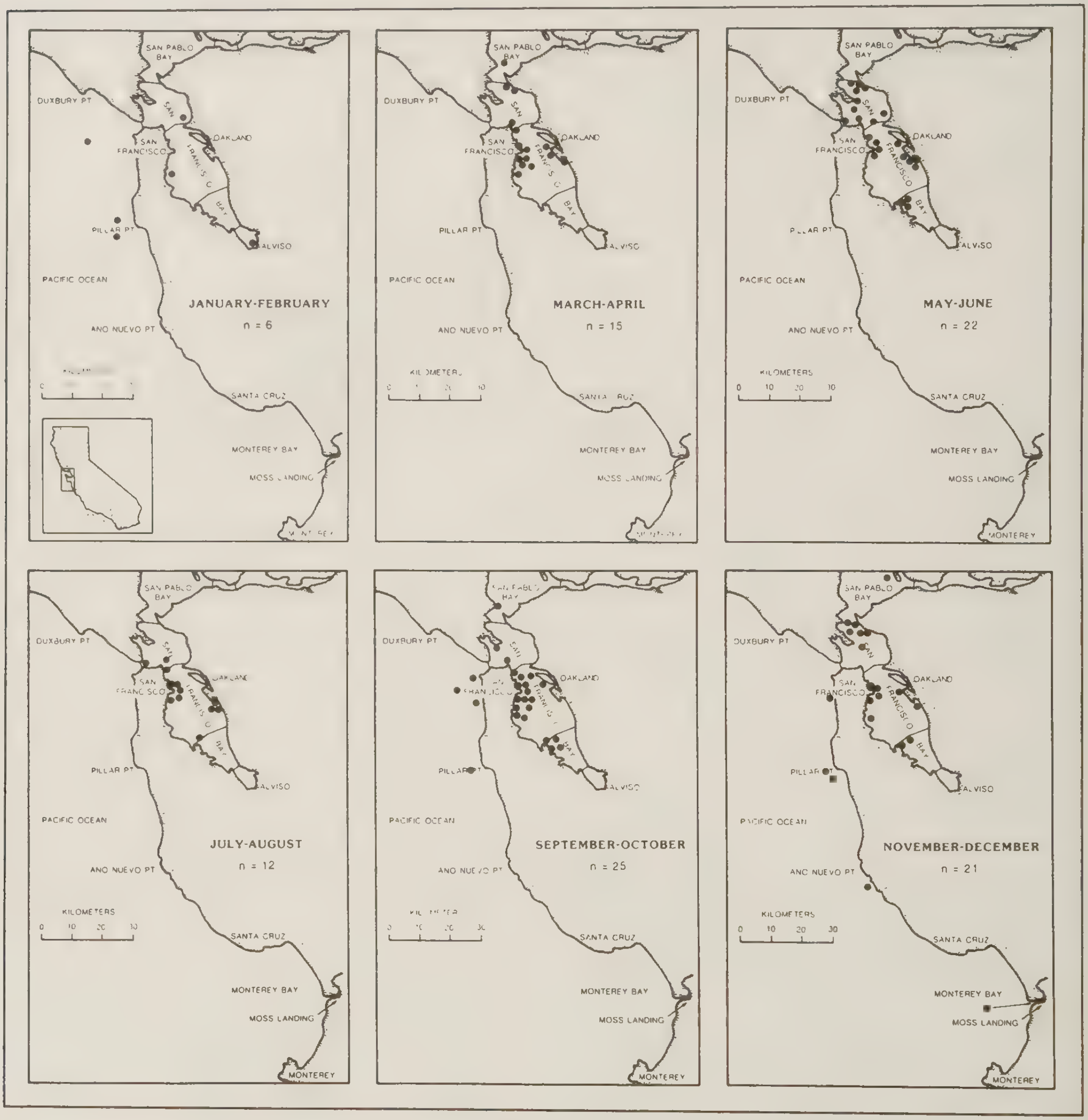
SAN PABLO BAY
DUXBURY PT
SAN FRANCISCO
OAKLAND
SAN FRANCISCO BAY
PILLAR PT
ALVISO
PACIFIC OCEAN
ANO NUEVO PT
SANTA CRUZ
MONTEREY BAY
MOSS LANDING
MONTEREY
KILOMETERS
0 10 20 30
JANUARY-FEBRUARY
n = 6
MARCH-APRIL
n = 15
MAY-JUNE
n = 22
JULY-AUGUST
n = 12
SEPTEMBER-OCTOBER
n = 25
NOVEMBER-DECEMBER
n = 21

Figure 3

Bimonthly distribution of leopard shark recoveries in and around San Francisco Bay, California, 1979–88, for which recapture location and date were known.

Of the recoveries, 81.5% were reported by sport anglers, 12.0% by commercial fishermen, and 6.5% of the fish were found on shore or had an unknown recapture method. Those recovered by recreational anglers were rather evenly divided between shore and boat anglers, with skiff fishermen dominating the latter category. The important role of recreational anglers in the recovery of tagged fish appears to reemphasize the predominance of recreational users of the leopard shark resource.

Over the 9-year period, most fish were recaptured during the months of September (20%) and June (13%);

the fewest were returned in February (2%), January (4%), and July (5%). The return rate for 'healthy' fish was 9.9% and that of 'injured' fish, 15.8%. Clearly, there is no indication that handling during the tagging process induced excess tagging mortality. The sex ratio of recaptured fish was exactly the same as at tagging (53% males) indicating little if any selective mortality with regard to sex.

Movements

Bimonthly distribution patterns were plotted using recapture information from 101 recoveries made during 1979–88, for which recapture location and date were known (Fig. 3). From about March through August recoveries were restricted to the bay, while from September through February a marked pattern of dispersal occurred within and outside of the bay. One shark traveled as far as Elkhorn Slough near Monterey, about 140 km south of the entrance to San Francisco Bay.

To discern year-to-year differences in the temporal and general geographic pattern, Table 4 shows recoveries by year and recapture area (south San Francisco Bay, central and north bays, ocean/outside bay). The year 1983 was unique in that the greatest number of recoveries in any one year was made that year (22 fish, plus 2 fish recovered dead). It was also the only year that ocean recoveries were made as early as September, and the only year when an unusual number of recoveries (6 fish) was made in the central bay in June. (During the 9-year study period, there was only one other instance, in 1981, of a fish being taken in the central bay in June.)

No distribution pattern appeared to be correlated with fish size or sex, but due to the small sample size, the results do not preclude the possibility that the pattern may vary with sexual maturity or age. The sex ratio of fish taken in the ocean was normal (1:1); however, one commercial fisherman, who caught 3 of the 12 tagged fish taken in the ocean, reported that all 3 were gillnetted from the same depression on the sea floor in Half Moon Bay (one taken 13 Nov. 82, the other two taken in 1986 on 20 Oct. and 17 Nov.), and all 3 were large females with developing embryos.

Table 4

Distribution of leopard shark tag recaptures in and around San Francisco Bay, California, by year and area of recapture for which date and recovery area are known.

	Area of recapture			
Calendar year of recapture	South bay	Central & north bays	Outside bay/ ocean	Totals
1979	10	2	1	13
1980	8	9	0	17
1981	11	1	1	13
1982	5	4	3	12
1983	9	9	4	22
1984	9	2	0	11
1985	2	2	0	4
1986	1	0	3	4
1987	2	0	0	2
1988	3	0	0	3
Total	60	29	12	101

Mortality rates and virtual population analysis

The oldest ages reported for this species are 24 years for a male of approximately 135 cm in length and 20 years for a 130-cm female (Kusher 1987, fig. 8). However, we arbitrarily decided to use a maximum age of 30 years in Hoenig's (1983) regression equation since there are records of fish larger (180 cm; Kato et al. 1967) than those that were aged; we also noted that the largest female aged by Kusher (140 cm) was, at 18 years, not the oldest. Because the largest fish cited above was taken prior to the time when there was more than nominal fishing directed at this species, we feel that M may be assumed approximately equal to the Z from Hoenig's regression equation. The result of taking $t_{max} = 30$ in the equation was an estimated M of 0.14.

While we have no explicit estimate of a tag-shedding rate from this experiment, the results of Kato and Carvallo (1967) from multiple tagging of sharks at the Revillagigedo Islands, Mexico, indicated a minimal annual shedding rate of 0.095. We have taken this value, converted it to an annual instantaneous loss rate of 0.10, and added it to the previously estimated 0.14 to obtain $X = M + 0.1 = 0.24$ for use in lieu of natural mortality in the VPA. We assume, and believe it reasonable given the apparent hardiness of the animals and toughness of their skin, that there was no instantaneous (type I) tag shedding.

With regard to the percent of tag recoveries reported to us, we again have no "built-in" estimate, but the California Department of Fish and Game has conducted extensive studies on the return rates for various reward levels associated with tagged striped bass in the same general area that the leopard shark tagging occurred (Stevens et al. 1985). Based on their experience (D. Kohlhorst, Calif. Dep. Fish Game, Stockton, CA 95205, pers. commun., Nov. 1988), it seemed that a 50% reporting rate would be the best value to use as an adjustment for tag recoveries in this case. To utilize this adjustment in the VPA, we use half the actual number of tag releases as the target for convergence.

Table 5

Leopard shark tag recoveries in and around San Francisco Bay, California, including natural mortality (M), estimated fishing mortality (F), and rate of exploitation (E), by post-tagging annual time intervals.

Time interval	Recovery period	Tags recovered	Assumed $M+0.1$	F	E
1	10/1/79–9/30/80	25	0.24	0.061	0.055
2	10/1/80–9/30/81	18	0.24	0.059	0.054
3	10/1/81–9/30/82	12	0.24	0.053	0.048
4	10/1/82–9/30/83	26	0.24	0.163	0.141
5	10/1/83–9/30/84	13	0.24	0.119	0.105
6	10/1/84–9/30/85	3	0.24	0.038	0.035
7	10/1/85–9/30/86	3	0.24	0.050	0.046
8	10/1/86–9/30/87	5	0.24	0.116	0.103
9	10/1/87–9/30/88	3	0.24	0.099	0.088
	Total	108		$\bar{F}=0.084$	

Tag recoveries by yearly intervals after the release period, estimated annual instantaneous fishing and natural mortality coefficients, and rates of exploitation are shown in Table 5. Note that these are all of the tag recoveries which could be assigned to the time intervals; other tabulations of recoveries in this paper may differ because of various missing information components.

Yield and stock replacement per recruit

Shown in Figure 4 is the yield-per-recruit isopleth diagram for $M=0.28$ during the first year of life and 0.14 thereafter. Age at first capture ranges from 4 to 13 years, and F runs from 0.05 to 0.28. The graph indicates a fairly flat yield contour between $F=0.15$ and $F=0.28$, with age at first capture between 5 and 10 years.

Also in Figure 4 are isopleths showing percent population replacement per recruit over the same parameters used for the yield computations. For use in calculating population replacement, the fitted curve (Fig. 5) relating Ackerman's data on number of embryos to parental weight was

$$P_t = 22.64 - (7592)\,(0.4208)^{w(t)},$$

where P_t is number of embryos, $w(t)$ is maternal weight (kg) at age t, and the standard error of estimate equals 0.38313. The value for $w(t)$ was obtained from

$$w(t) = 0.00000305 \times \{172.4[1-\exp(-0.0717[t+2.302])]\}^{3.05}.$$

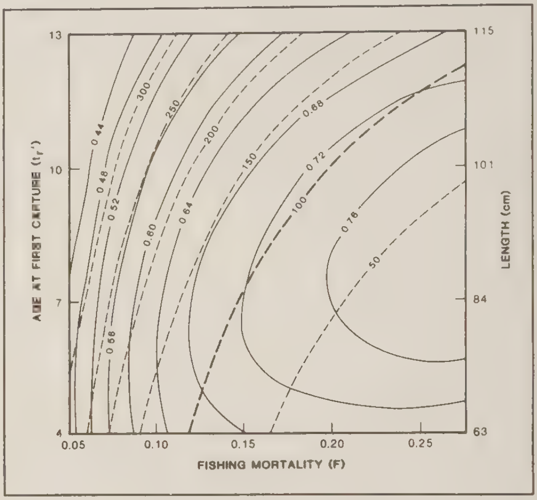

Figure 4

Isopleths showing percent population replacement of leopard sharks tagged in San Francisco Bay, California, in numbers (dashed lines) and yield per recruit in kilograms (solid lines), for $M=0.28$ during the first year of life and 0.14 thereafter.

Replacement increases steadily as F tends toward 0 and age at first capture increases (equation 2). The shape of this surface is not unexpected, but clearly some type of density-related compensation would be needed to increase mortality or reduce fecundity as the population increases; otherwise in the absence of fishing the sea would be filled with leopard sharks. This mechanism might be in the form of higher juvenile mortality, less frequent litter bearing, or reduced average litter size. Holden (1973, 1977) discusses some possible mechanisms of this type and cites examples from the literature of marine mammals and elasmobranchs. We do not have information to examine any of these possibilities in the present case.

Discussion

If it is assumed that the tagged population approximates the real population, these results suggest that San Francisco Bay leopard sharks are mostly resident, with some moving out of the bay during fall and winter. Judging from the single Moss Landing recovery, limited population exchange evidently occurs between Elkhorn Slough and San Francisco Bay leopard sharks. Also, previously undocumented evidence was received during the course of this study from L. Talent (Oklahoma State Univ., Stillwater, OK 74078, pers. commun., July

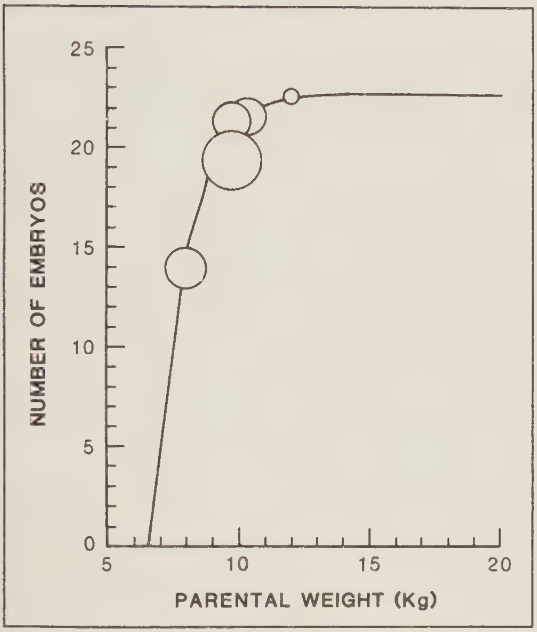

Figure 5
Fitted monomolecular curve relating mean number of leopard shark embryos in litters to parental weight. Areas of symbols are proportional to weighting factors of points used in the fitting process.

1982), who reported that a leopard shark tagged by him in December 1971 in Elkhorn Slough, Moss Landing, California, was recaptured February 1973 in south San Francisco Bay.

It is not known to what extent fishing effort influenced the recapture pattern, because effort information on the commercial and recreational catch is not available to the degree of geographic precision needed for such an analysis. We do know that leopard sharks are susceptible to bottom fishing gear, whether it be baited hook, gillnet, or, to a lesser extent, bottom trawl. Judging from the available data on recreational and commercial landings, and the much greater proportion of recreational versus commercial tag recaptures, recreational anglers are the primary users of the leopard shark resource in northern California. Angling for bottom fishes takes place in most areas inside the bay system year-round (Squire and Smith 1977), although in winter, inclement weather may lower fishing effort within the bay as well as along the open coast. Bottom-fishing effort in the ocean is thought to be comparatively less than in the Bay at least in waters shallower than 91 meters, the reported depth range of this species.

The 1983 peak in the tagged fish recovery rate and the associated rise in fishing mortality that we calculated (Tables 4 and 5) was unexpected. We have no evidence that fishing effort increased that year to cause this jump in the tag return rate, but there was a substantial rise in the California commercial catch of leopard shark that year, primarily driven by an increase in San Francisco landings (Table 1). There was also a similar rise in the estimated recreational catch (Table 2). The year 1983 was also one of unusual oceanographic conditions, when warm, nutrient-poor El Niño water intruded along the central California coast (McClain 1983, Norton et al. 1985). These El Niño conditions may have caused an influx of sharks from more southerly populations, but the increased rate of recovery for San Francisco Bay tagged fish should be independent of immigration of fish from other areas.

The California Department of Fish and Game (1987) and Pearson (1989), conducting trawl surveys of San Francisco Bay fishes, have observed higher trawl catches of leopard sharks during wet as opposed to dry years, and 1983 was indeed a wet year. That year the bay system experienced the highest delta outflows from the Sacramento-San Joaquin River systems in over 10 years, and June freshwater outflows were twice that of the previous wet year of 1982 and six times the previous decade's average outflow for that month (Calif. Dep. Water Resour., DAYFLOW Prog. Summ., Sacramento, CA 95816, Sept. 1987). Perhaps the anomalous conditions affected the local distribution and availability of central California leopard sharks and possibly their benthic prey, making the sharks more vulnerable to centers of fishing pressure.

In estimating the mortality, yield, and stock-replacement values, it was neccessary to make many assumptions and adjustments. Clearly we must assume that the tagged fish rapidly mix with the balance of a relatively closed San Francisco Bay population, and that tagged and untagged animals are equally likely to be caught. But because of the paucity of this type of information on these animals, an apparent high susceptibility of elasmobranch stocks to fishing pressure, and the noticeable increase in fisheries targeting on sharks, we felt it appropriate to present our best estimates based on the available data and current knowledge of elasmobranch biology.

In the case of the leopard shark, high stock maintenance is surely more important than a large yield per recruit. And while there is obviously something wrong with the stock replacement values which exceed 100% on an equilibrium basis, we would like to accept the 100% isopleth as reasonably valid. Noting in Table 5 that estimated F's ranged from 0.038 to 0.163 with a mean of 0.084, and observing in Figure 4 that the 100% replacement isopleth runs well to the right of the

0.68-kg isopleth over the higher observed levels of fishing mortality, it appears that management for full stock replacement would not involve a very great loss of yield per recruit. In fact, assuming an F of 0.2 and an age of first capture of 10 years, which equates to a 100-cm (40-inch) size limit, yield per recruit is less than 10% below the maximum shown in Figure 4. And given any F between the mean estimated value of 0.084 and the maximum estimate of F, the yield with the 100-cm size limit is within 10% of the maximum for that F.

However, in terms of numbers caught per recruit there is a substantial decline as the size limit increases. At $F = 0.2$, numbers per recruit values are 0.126, 0.192, and 0.292 for size limits of 100, 84, and 63 cm respectively; corresponding mean weights of fish comprising the retained catch are 5.8, 4.0, and 2.4 kg. All of these estimates assume that mortalities due to hooking and releasing undersized fish are negligible.

Based on the above information, a viable management strategy for the leopard shark would appear to be a size limit of 40 inches (100 cm). Although this size limit results in a 34% decline in numbers caught compared with a 33-inch (84 cm) limit, the fish which can be kept are almost 50% larger. Further, stock replacement is at the 100% level as compared with only 55% at the smaller size limit.

We stress, however, that our mortality and fecundity estimates were based on data from studies in only one area within the animal's geographic range, and the extent to which these can be extrapolated to the entire coastal population is not known.

Acknowledgments

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Citations

Ackerman, L.T.
1971 Contributions to the biology of the leopard shark, *Triakis semifasciata* (Girard) in Elkhorn Slough, Monterey Bay, California. M.A. thesis, Sacramento State College, Sacramento, CA, 54 p.

California Department of Fish and Game
1987 Delta outflow effects on the abundance and distribution of San Francisco Bay fish and invertebrates, 1980–1985. DFG Exhibit 60 entered by the California Department of Fish and Game for the State Water Resources Control Board. 1987 Water Quality/Water Rights Proceeding on the San Francisco Bay/Sacramento-San Joaquin Delta. Bay-Delta Project, Calif. Dep. Fish Game, Stockton, CA 95205, 345 p.

Compagno, L.J.V.
1984 Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Species Catalogue, Vol. 4, Parts 1 and 2. FAO Fish. Synop. 125, 4 (1 & 2), 655 p.

Eschmeyer, W.H., E.S. Herald, and H. Hammann
1983 A field guide to the Pacific coast fishes of North America from the Gulf of Alaska to Baja California. Houghton Mifflin Co., Boston, 336 p.

Frey, H.W. (editor)
1971 California's living marine resources and their utilization. Calif. Dep. Fish Game, Sacramento, 148 p.

Fry, F.E.J.
1949 Statistics of a lake trout fishery. Biometrics 5(1):27–67.

Gulland, J.A.
1965 Estimation of mortality rates. Annex to Arctic Fisheries Working Group Rep., Int. Counc. Explor. Sea C.M. 1965, Doc. 3, 9 p. (mimeo).
1983 Fish stock assessment: A manual of basic methods. Wiley, NY, 223 p.

Hoenig, J.M.
1983 Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 81:898–903.

Holden, M.J.
1973 Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164:360–367.
1974 Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* Harden-Jones, F.R. (ed.), Sea fisheries research, p. 117–137. Wiley, NY.
1977 Elasmobranchs. *In* Gulland, J.A. (ed.), Fish population dynamics, p. 187–215. Wiley, NY.

Holts, D.B.
1988 Review of U.S. west coast commercial shark fisheries. Mar. Fish. Rev. 50(1):1–8.

Kato, S., and A.H. Carvallo
1967 Shark tagging in the eastern Pacific Ocean, 1962–65. *In* Gilbert, P.W., R.F. Mathewson, and D.P. Rall (eds.), Sharks, skates and rays, p. 93–109. Johns Hopkins Press, Baltimore.

Kato, S., S. Springer, and M. Wagner
1967 Field guide to eastern Pacific and Hawaiian sharks. U.S. Fish Wildl. Serv., Circ. 271, 47 p.

Kusher, D.I.
1987 Age and growth of leopard sharks, *Triakis semifasciata* from central California. M.S. thesis, San Francisco State Univ., 35 p.

Kusher, D.I., S.E. Smith, and G.M. Cailliet
In prep. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Moss Landing Mar. Lab., P.O. Box 450, Moss Landing, CA 95039.

McLain, D.R.
1983 Coastal ocean warming in the northeast Pacific, 1976–83. *In* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 61–86. Rep. ORESU-W-83-001, Oregon State Univ., Sea Grant Prog., Newport.

Murphy, G.I.
1965 A solution of the catch equation. J. Fish. Res. Board Can. 22:191–202.

Norton, J., D. McLain, R. Brainard, and D. Husby
1985 The 1982–83 El Niño event off Baja and Alta California and its ocean context. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: El Niño effects in the eastern subarctic Pacific Ocean, p. 44–72. Rep. WSG-WO 85-3, Wash. Sea Grant, Univ. Wash., Seattle.

Pearson, D.E.
1989 Survey of fishes and water properties of South San Francisco Bay, California, 1973–82. NOAA Tech. Rep. NMFS-78, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., 21 p.

Ristori, A.
1987 An overview of U.S. sport shark fisheries. *In* Cook, S. (ed.), Proceedings, Sharks: An inquiry into biology, behavior, fisheries, and use, p. 231–234. Oregon State Univ. Ext. Serv., Corvallis.

Russo, R.A.
1975 Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*). Calif. Fish Game 61:95–103.

Slosser, V.
1987 U.S. shark fisheries and markets. *In* Cook, S. (ed.), Proceedings, Sharks: An inquiry into biology, behavior, fisheries, and use, p. 131–135. Oregon State Univ. Ext. Serv., Corvallis.

Smith, S.E.
1984 Timing of vertebral band deposition in tetracycline-injected leopard sharks. Trans. Am. Fish. Soc. 113:308–313.

Springer, S.
1960 Natural history of the sandbar shark *Eulamia milberti*. U.S. Fish Wildl. Serv., Fish. Bull. 61(178):1–38.
1967 Social organization of shark populations. *In* Gilbert, P.W., R.W. Mathewson, and D.P. Rall (eds.), Sharks, skates, and rays, p. 149–174. Johns Hopkins Press, Baltimore.

Squire, J.L., Jr., and S.E. Smith
1977 Anglers' guide to the United States Pacific coast. Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Seattle, 139 p.

Stevens, D.E., D.W. Kohlhorst, L.W. Miller, and D.W. Kelley
1985 The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Trans. Am. Fish. Soc. 114:12–30.

Talent, L.G.
1976 Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Calif. Fish Game 62:286–298.

Tomlinson, P.K.
1970 A generalization of the Murphy catch equation. J. Fish. Res. Board Can. 27:821–825.

9058

Baitfish Stock Assessment Using the Egg Production Method: an application on the Hawaiian anchovy or nehu (*Encrasicholina purpurea*)

D.A. Somerton*

Abstract

The biomass of nehu (*Encrasicholina purpurea*) in Pearl Harbor was estimated weekly, over a two year period, using a new stock assessment procedure known as the Egg Production Method (EPM). Although the EPM was originally developed for assessing relatively long-lived, temperate anchovies (Northern Anchovy and Anchovetta), it has proven to be a low-cost, effective way of assessing the abundance of nehu, a short-lived, tropical stolephorid anchovy. The effectiveness of the EPM is largely the result of its being based on the life history stage that is the least aggregated and easiest to sample, that is, the egg stage. Because of this, the biomass estimates obtained using the EPM are less influenced by environmental fluctuations than estimates obtained using commercial catch statistics. Over the study period, nehu spawning stock biomass varied between 0.5 and 5.0 tonnes and was clearly associated with the variation in the rate of nehu bait catch for the pole-and-line tuna fishery. Stock variation also was associated with seasonal variation in reproductive output, primarily changes in weight-specific fecundity and spawning frequency and in the survival rate from the egg stage through the first feeding larvae.

Stock assessment of baitfishes is difficult because fishery-dependent information such as catch per unit effort is often not a good indicator of relative abundance (Wetherall 1977), and fishery-independent information such as hydroacoustic data is expensive to obtain. One promising new approach, called the Egg Production Method (EPM), was developed to assess the biomass of small schooling species from the abundance of their pelagic eggs. The basic concepts of the EPM were first developed by Saville (1964) and later elaborated by Parker (1980). The estimate of biomass can be expressed algebraically as:

$$B = \frac{P}{F\,R} \qquad \text{Equation 1}$$

where B is the biomass, P is the daily production of eggs by the population, F is the fecundity per gram body weight of spawning females, and R is the proportion, by weight, of spawning females in the population. Definition of the population, and therefore the calculation of R, can be in terms of mature fish (spawning stock) or fish larger than some minimum size (commercial stock). In practice, P is estimated by sampling pelagic eggs with a plankton net and F and R are estimated by sampling adult fish.

The EPM was initially applied to the California anchovy (*Engraulis mordax*; Lasker 1985) and anchovetta (*E. ringens*; Alheit 1985), both relatively large, long-lived, temperate species, but it is also ideally suited for stock assessment of the smaller, shorter-lived anchovies and sprats used as baitfishes by the tuna pole-and-line fisheries. One such species is the Hawaiian anchovy or nehu (*Encrasicholina purpurea*). Nehu are endemic to the Hawaiian Islands and occur exclusively within enclosed bays, especially those that receive significant freshwater input. Typical of many tropical stolephorid anchovies (Dalzell 1987), nehu are short-lived (Struhsaker and Uchiyama 1976) and spawn almost continuously throughout the year (Tester 1955, Clarke 1987). Unlike most other baitfishes, however, nehu occur in shallow, turbid areas during the day and migrate at night to deeper, clearer areas where they spawn and feed. The commercial fishery exploits this unusual behaviour and captures nehu with seines in their shallow daytime habitat (Uchida 1977).

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In this paper an application of the EPM is applied to a population of nehu occurring within Pearl Harbor, Oahu, emphasising aspects which differentiate this from previous applications on temperate species. As nehu have a high biological turnover rate and are subjected to an intensive fishery, stock assessment must be frequent to resolve important aspects of population change. For this reason, nehu stock assessment surveys were conducted weekly rather than yearly as they have been for temperate species. In addition, the application of the EPM on nehu differed from previous studies (Picquelle and Stauffer 1985) in the methods used to estimate F and R. These differences primarily reflect the biological differences between nehu and temperate anchovies but also include measures intended to reduce the time requirements of sampling and sample processing.

Materials and Methods

Pearl Harbor was sampled weekly from 3 April 1986 to 7 April 1988. Each sampling day was separated into two periods: egg and plankton sampling and adult sampling. Eggs and plankton were sampled between 0700 and 1200 hours with a systematic sampling design (Cochran 1963) in which a single sample was taken near the geographic centre of each of 39 strata. The net used was 5 m long and 1 m in diameter at the mouth and constructed of 335 μm Nitex[1]. To allow its use from small boats, the net was not towed but instead was thrown overboard and sampled as it descended to the bottom (average depth of the sampling sites was about 12 m). Compared with a typical towed plankton net, our sampling net had two design features added to increase its effectiveness. First, to increase the sinking speed, lead weights (5 kg) were attached to the steel ring that held the mouth open. Second, to ensure closure of the net, a retrieval line was attached, not to the ring itself, but to a choke collar surrounding the net. Mesh bags of 335 μm Nitex were used as cod ends. When retrieved, these bags were sealed and placed in a 10% buffered formaldehyde solution.

In the laboratory, the plankton samples were examined without subsampling, and all nehu eggs and all large crustacean zooplankters, previously identified as preferred nehu food (Hiatt 1951), were counted. Egg and plankton densities at each station were estimated by dividing the counts by an estimate of the filtered volume computed as water depth multiplied by the mouth area of the net.

Adult nehu were sampled in a 1.5-hour period preceding sunset when the eggs to be spawned that evening were clearly hydrated and easily distinguished from unhydrated, mature eggs (Clarke 1987). Adults were captured, along with juveniles, using a beach seine of the same mesh size (9 mm) and design characteristics as a commercial nehu seine except that it was cut to approximately one-third scale (70 m long by 3 m deep) so that it could be set from a small boat. Nehu schools were located in their preferred daytime habitat, that is, shallow, turbid areas, with the same searching techniques used by commercial vessels. Schools were quickly surrounded with the seine, and a random sample of the catch was taken and immediately preserved in a 10% buffered formaldehyde solution.

In the laboratory, a subsample of nehu was drawn from each field sample: 1) An initial subsample of approximately 50 fish was randomly chosen. 2) In order of size, starting with the apparent largest individual, fish were removed from the subsample and examined microscopically for sex and stage of maturity. 3) If less than 25 mature females were obtained from the initial subsample, additional subsamples were drawn and examined completely in the same manner until at least 25 mature females were obtained. 4) To increase the speed of classifying fish, if six juveniles were drawn in succession from a subsample, all of the remaining fish in that subsample were also classified as juveniles without examination. Because individuals were chosen according to size, the remaining fish were smaller than any that had been visually classified and therefore were likely to be immature.

The criteria used to classify fish were based upon the following gross morphological features partly adapted from Clarke (1987):

- largest ova measuring $\geqslant$0.7 mm in length indicated a mature female with hydrated eggs;
- largest ova measuring 0.5–0.7 mm in length indicated a mature female with unhydrated eggs;
- testis depth (dorsal-ventral) measuring $\geqslant$ eye diameter indicated a mature male;

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[1] Reference to trade names does not imply endorsement by National Marine Fisheries Service, NOAA.

— largest ova measuring < 0.5 mm or testis depth measuring $<$ eye diameter indicated a juvenile.

After the subsample was chosen and classified, the following biological attributes were measured. Standard length (in millimetres) was measured for all mature fish and for the first 25 randomly chosen juveniles; any remaining juveniles were counted but not measured. Total body weight (in milligrams) was measured, after blot drying, for all fish measured for length except females with hydrated eggs; ovary-free body weight was measured for all females. Batch fecundity was estimated for females with hydrated eggs by teasing apart both of the ovaries and counting under a microscope all hydrated ova. Each count was replicated, and fecundity was estimated as the mean of the two counts. Over the 105 consecutive weeks of sampling, this process was repeated for each of 162 seine samples.

Data analysis and biomass estimation

Evaluation of Equation 1 requires estimates of *P*, *F*, and *R*. These estimates were obtained as follows. Daily egg production was estimated as

$$P = \Sigma\, D_i V_i; \qquad \text{Equation 2}$$

where D_i is the egg density at the ith station, and V_i is the volume of the ith stratum. The summation is over all 39 strata. Weight specific fecundity was estimated as

$$F = \frac{\Sigma E}{\Sigma W_{fh}} \qquad \text{Equation 3}$$

where ΣE is the sum of all hydrated ova, and ΣW_{fh} is the sum of the corrected total body weight of mature females with hydrated eggs. Spawning proportion was estimated as

$$R = \frac{\Sigma W_{fh}}{\Sigma W_m + \Sigma W_{fh} + \Sigma W_{fu}} \qquad \text{Equation 4}$$

where ΣW_m and ΣW_{fu} are the sums of the total body weights of males and of females with unhydrated eggs. The W_{fh} were corrected for the temporary weight gain due to egg hydration by regressing W_{fu} on ovary-free weight for females with unhydrated ovaries, then predicting W_{fh} from the ovary-free body weights of females with hydrated ovaries. When the commercial population rather than the spawning population was estimated, Equation 4 was modified slightly to include in the denominator the term ΣW_j or the sum of the total body weights of juveniles.

Variance and bias of the estimated biomass were approximated by using the delta method (Seber 1973). The variance estimator was

$$V(B) = B^2[CV(P)^2 + CV(F)^2 + CV(R)^2]; \qquad \text{Equation 5}$$

and the bias estimator was

$$\text{bias}(B) = B[CV(F)^2 + CV(R)^2]; \qquad \text{Equation 6}$$

where *CV* represents the coefficient of variation.

The variances needed to evaluate Equations 5 and 6 were estimated as follows. The variance of the daily egg production, *P*, was calculated as

$$V(P) = \Sigma V_i^2 V(D_i); \qquad \text{Equation 7}$$

where $V(D_i)$ was approximated as the variance in D_i among three adjacent stations, because the plankton net samples were not replicated at each station. The variances of the biological parameters were estimated as

$$V(\bar{X}) = \frac{\Sigma(X_i - \bar{X})^2}{N(N-1)} \qquad \text{Equation 8}$$

where X_i is the ith sample mean for one of the biological parameters and $\bar{X}$ is the mean of N sample means. Since the number of samples collected each week was always small and sometimes even insufficient to estimate variance, the weekly estimates of the means and variances of the biological parameters were calculated from a pool of all samples within a 5-week moving time window centred on the particular week.

Results and Discussion

Biomass estimates

Weekly spawning and commercial biomass estimates (Figure 1) had similar patterns of variation over time, but the commercial biomass estimates were always larger with wider confidence intervals. Over the 2-year period, the population fluctuated seasonally with maximum abundance in March-April and perhaps again in late July-August and a minimum in November. This pattern of variation was similar to that observed in the abundance of nehu eggs in Kaneohe Bay, Oahu (Tester, 1955).

Egg production

Estimates of daily egg production can be influenced by two sources of bias. First, an overestimation can occur if the eggs of other fishes are misidentified as the target species. For nehu, such misidentification is unlikely because no other fishes in Pearl Harbor have eggs similar to those of nehu (Tester 1951; Clarke 1987). However, in areas where several closely related species spawn

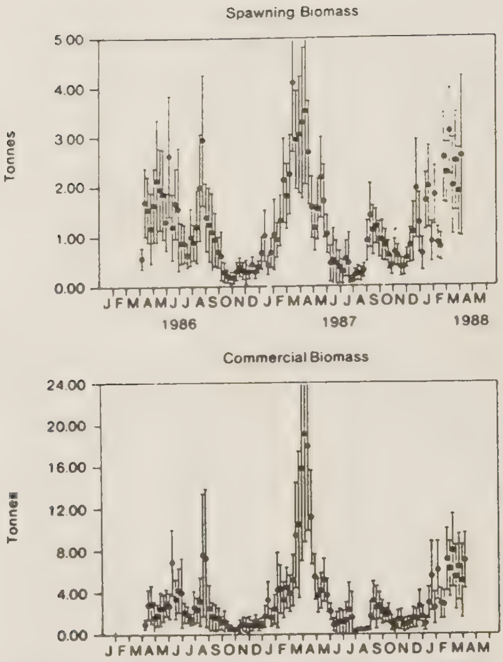

Figure 1. Weekly estimates and 95% confidence intervals of the spawning and commercial biomasses of nehu within Pearl Harbor in metric tonnes.

concurrently, egg identification may be problematical. Second, an underestimation can occur if egg mortality is high and the time between spawning and sampling is large. In northern anchovy, for example, the egg mortality rate was estimated at 53% per day (Smith and Lasker 1978), but we believe that nehu egg mortality is substantially less.

Egg mortality can be attributed to either predation or abnormal embryological development. Predation by the adults accounted for 32% of the egg mortality in northern anchovy (Hunter and Kimbrell 1980) but is probably much lower in nehu because eggs are rarely found in adult gut samples (Hiatt 1951). Mortality due to abnormal development could be significant in nehu but would be difficult to quantify because, based on our preliminary studies of egg density, dead nehu eggs sink rapidly in water with densities typical of Pearl Harbor and thus, are likely to escape capture. Because some egg mortality is likely, we believe that our estimates of egg production, based on the abundance of eggs roughly 16 hours after spawning, may be too low.

Reproductive parameters

Previous applications of the EPM (Alheit 1985; Hunter and Macewicz 1985) have used postovulatory follicles to identify spawning females. Instead, we chose to use the presence of hydrated eggs, primarily because histological preparation is not required and identification is, therefore, faster and easier. The use of hydrated ova, however, imposes a restriction on the time that the population can be sampled, to ensure correct identification of spawning females. This restriction reduces the level of precision in the biomass estimates that might have otherwise been achieved and subjects the estimates of spawning proportion to a potential bias.

The appropriate period for sampling adults is bounded between the time of day when hydrated ova are sufficiently enlarged to be recognisable and sunset when migration to deeper water begins (Clarke 1987). Recognisable hydrated ova may occasionally be observed during the early afternoon, but Clarke (1987) has found that not until two hours before sunset did all prespawning females have some ova ⩾ 0.7 mm. Since the definition of the correct time window for sampling is so important, our study repeated part of Clarke's (1987) study by sampling adult nehu at approximately half-hour intervals throughout the late afternoon and found that a smaller time window of 1.5 hours was required to ensure correct identification. This time period was so short that we were only able to obtain an average of 1.6 adult samples each week and occasionally experienced periods in which no samples could be obtained.

Not only is the time period for adults sampling short, but it occurs immediately before spawning when segregation of sexually active and inactive fish may occur. Previous studies on northern anchovy (Picquelle and Stauffer 1985) and anchovetta (Alheit 1985) have found that active females segregate from inactive females and aggregate with males near the time of spawning. For nehu, segregation of active from inactive females, aggregation of active females with males, and segregation of adults from juveniles were tested and all were highly significant (chi-square test of homogeneity; $P<0.001$). This means that some segregation had occurred by the time the adult sampling period began. Such segregation increases biological heterogeneity among schools, and thereby increases the variance in the estimates of the proportion spawning.

In addition to its influence on the precision of the biomass estimates, the use of hydrated ova to identify spawning females is subject to one important source of sampling bias: differential catchability between sexually active and inactive females. For both northern anchovy (Picquelle and Stauffer 1985) and anchovetta (Alheit 1985), active females have a higher vulnerability to the sampling gear, perhaps due to a difference either in net avoidance or in depth distribution. For nehu, however, active and inactive females are apparently equally vulnerable, at least during the adult sampling period, because both occur in the shallow, nearshore areas sampled during the day (Clarke 1987). Furthermore, using postovulatory follicles and estimated rates of ova development from fish sampled at all times of day, Clarke (1987) estimated that individual nehu spawn every other day or, expressed as the inverse, that nehu have a daily spawning proportion of approximately 0.50. Since our estimate of mean proportion spawning, 0.53 (95% confidence interval, ± .04), is not significantly different from Clarke's (1987), it is unlikely that our sampling was biased.

Considerations for other baitfish applications

Other applications of the EPM on baitfishes are likely to also require frequent sampling, but lack sufficient resources for processing a large number of adult samples. Our approach to this problem was to save time by using hydrated ova rather than postovulatory follicles to identify spawning females. However, other shortcuts could be taken, especially when there is little temporal variation in adult parameters. One approach is to save time in sampling and sample processing by calculating biomass estimates based on long-term mean parameter values instead of weekly estimates. To determine how accurate such biomass estimates would have been for nehu, we compared the estimates calculated using the smoothed parameter values to those computed using the overall mean parameter values. The results indicated that roughly 58% of the variability in spawning biomass and 35% of the variability in commercial biomass were explained by the variability in the biomass estimates computed from long-term means. Much of the loss in predictability, however, was at high frequencies, while most of the low frequency and seasonal fluctuations are preserved (Fig. 2). For still further savings in time, this approach could be extended by simply eliminating adult sampling altogether and treating egg abundance as a proxy for fish abundance similar to the way catch per unit effort is used.

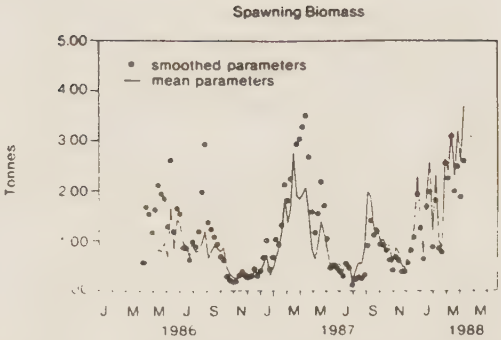

Figure 2. Spawning biomass calculated by using the smoothed weekly mean estimates of the adult parameters (F and R) and by using the total overall mean of the adult parameters.

Factors influencing nehu population fluctuations

Since the nehu population in Pearl Harbor is closed, receiving little or no immigration (Tester and Hiatt 1952), the observed variation in abundance (Fig. 1) must be due to variations in the recruitment of juveniles and the mortality rate of adults. Recruitment to the nehu population depends to some degree upon the biomass of adult females, the production of feeding larvae per gram of female, and the survival of feeding larvae to adulthood. Although survival of feeding larvae in our study was not considered, the variation in larval production was examined. Larval production per gram of female can be considered as the product of three components: 1) the production of eggs per gram of female body weight (Fig. 3d), 2) the proportion of the population spawning each day (Fig. 3c), and 3) the survival of eggs through the stage of first feeding larvae (Fig. 3e). All three of these components are seasonal, but their product, that is, the production of feeding larvae per gram of adult female (Fig. 3f) has a conspicuously strong seasonal pattern that is similar to those of the mean water temperature within Pearl Harbor (Fig. 3a) and to the density of the crustacean zooplankters that are the primary component of nehu food (Fig. 3b).

The total mortality rate of adults is the sum of both natural and fishing mortalities. Based on our preliminary studies of the Pearl Harbor population, natural mortality appears to be nearly constant over time, but fishing mortality varies greatly. Since the catch rises and falls almost synchronously with the estimated spawning biomass (Fig. 1), the fishery is bait limited and responds quickly to changes in bait availability. This response occurs in two ways. First, when bait abundance increases, the bait catch of individual vessels tends to increase, at least until capacity is reached. Second, more vessels fish in Pearl Harbor when the catch rates there are high relative to other baitfishing areas. The link between changes

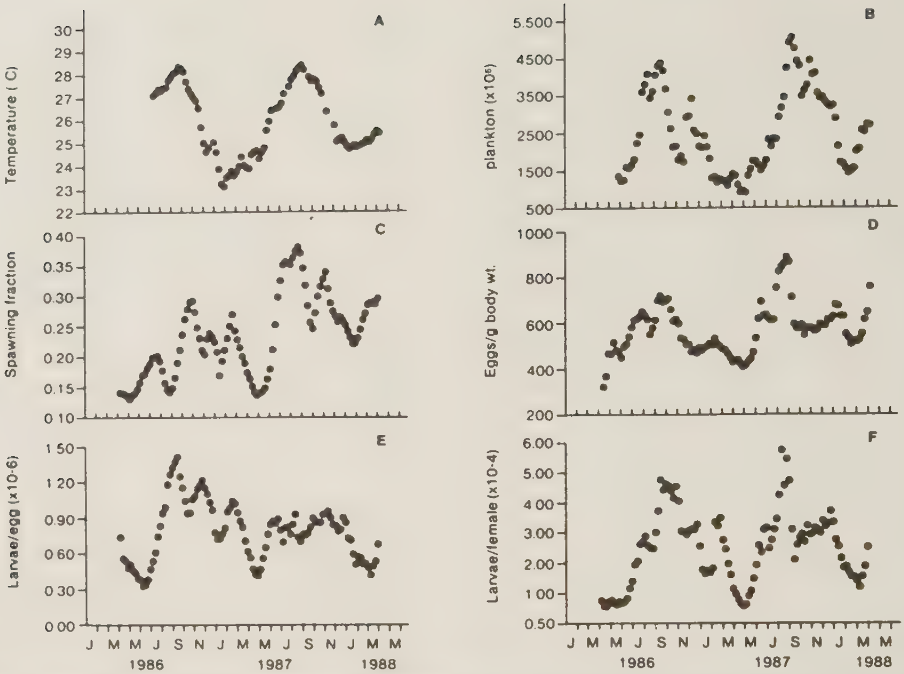

Figure 3. Weekly estimates of A) mean water temperature in Pearl Harbor, B) total abundance of all crustacean zooplankters identified as nehu food, C) proportion of the population, by weight, comprised of spawning females, D) batch fecundity expressed as eggs per gram body weight of spawning female, E) a crude estimate of early larval survival calculated as the total number of feeding larvae caught in one week divided by the number of eggs produced in the previous week, and F) number of feeding larvae produced by 1 gm of spawning female, that is, the product of C, D, and E.

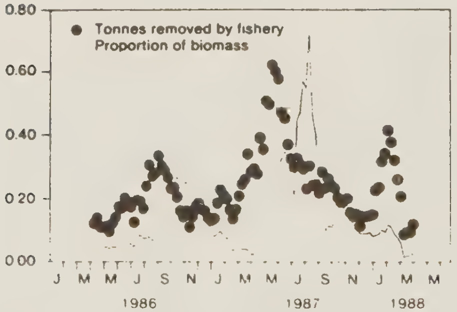

Figure 4. Catch of nehu within Pearl Harbor, expressed in tonnes and as a proportion of the estimated commercial biomass. This proportion is also known as the exploitation rate.

in effort and changes in nehu abundance is subject to inertia, and for a time, effort can remain high, or even increase, when the population begins to fall. As a result, the proportion of the population taken, or the exploitation rate, increases markedly (Fig. 4) and the abundance of nehu rapidly falls.

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References

Alheit, J. 1985. Spawning frequency of Peruvian anchovies taken with a purse seine. In: R. Lasker ed., An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy. *Engraulis mordax*, U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 59–61.

Clarke, T.A. 1987. Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85, 127–138.

Cochran, W.G. 1963. Sampling techniques. John Wiley & Sons, Inc., N.Y., 413 p.

Dalzell, P. 1987. Some aspects of the reproductive biology of Stolephorid anchovies from northern Papua New Guinea. Asian Fish. Sci. 1, 91–106.

Hiatt, R.W. 1951. Food and feeding habits of the nehu, *Stolephorus purpureus* Fowler. Pac. Sci. 5, 347–358.

Hunter, J.R., and Kimbrell, C.A. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78, 541–544.

Hunter, J.R., and Macewicz, B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. In: R. Lasker ed., An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 79–94.

Lasker, R. ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 99 p.

Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78, 5541–44.

Picquelle, S., and Stauffer, G. 1985. Parameter estimation for an egg production method of anchovy biomass assessment. In: R. Lasker ed., An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 7–15.

Saville, A. 1964. Estimation of the abundance of a fish stock from egg and larval surveys. In: J.A. Gulland ed., On the measurement of abundance of fish stocks, Rapp. P.-v. Reun. Cons. Int. Explor. Mer 155, 164–170.

Seber, G.A.F. 1973. The estimation of animal abundance and related parameters. Hafner Press, N.Y., 506 p.

Smith, P.E. and Lasker, R. 1978. Position of larval fish in an ecosystem. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 173, 77–84.

Struhsaker, P. and Uchiyama, J.H. 1976. Age and growth of the nehu, *Stelophorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74, 9–17.

Tester, A.L. 1951. The distribution of eggs and larvae of the anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, with a consideration of the sampling problem. Pac. Sci. 5, 321–346.

1955. Variation in egg and larva production of the anchovy, *Stolephorus purpureus* Fowler, in Kaneohe Bay, Oahu, during 1950–1952. Pac. Sci. 9, 31–41.

Tester, A.L. and Hiatt, R.W. 1952. Variation in the vertebral number of the anchovy (*Stolephorus purpureus*) in Hawaiian waters. Pac. Sci. 6, 59–70.

Uchida, R.N. 1977. The fishery for nehu, *Stolephorus purpureus*, a live bait used for skipjack tuna, *Katsuwonus pelamis*, fishing in Hawaii. In: R.S. Shomura ed. Collection of tuna baitfish papers, U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408, 57–62.

Wetherall, J.A. 1977. Catch statistics and abundance of nehu, *Stolephorus purpureus*, in Kaneohe Bay. In: R.S. Shomura ed. Collection of tuna baitfish papers, U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 408, 114–118.

9059

Distribution and Apparent Abundance of the Basking Shark, *Cetorhinus maximus*, off the Central and Southern California Coast, 1962-85

JAMES L. SQUIRE, Jr.

Background

Basking sharks, *Cetorhinus maximus*, are frequently observed along the central and northwestern southern California coast during the winter and spring months. These large plankton feeding elasmobranchs, second in size only to the whale shark, *Rhineodon typus*, had been the subject of a small commercial fishery off California in the late 1940's and early 1950's for their liver oil, rich in vitamin A, and in later years for reduction into fish meal and oil (Roedel and Ripley, 1950). These fisheries were sporadic and did not take basking sharks in large numbers.

Along the west coast of North America, the other substantial amount of "fishing" occurred in the 1950's when an eradication program was conducted in British Columbia waters by the Canadian Fisheries Department. Basking sharks were damaging Pacific salmon, *Oncorhynchus* spp., gill nets and a boat equipped with a sharp plow-like device was used to ram and kill basking sharks. About 50 sharks were reported killed during the first month of operation (Anonymous, 1956).

Basking sharks are fished by harpoon in many areas of the world (Norway, Ireland, Scotland, Iceland, China, Japan, Peru and Ecuador). These fisheries are reported to be sporadic due to periodic depletion of basking shark stocks (Compagno, 1984). Basking shark meat is used for human consumption, fresh or dried salted. The fins are used for shark-fin soup, the liver for squalene, the hide for leather, and the carcasses for fish meal (Compagno, 1984).

Observations on the occurrence of these sharks off central California, based on records of Edward Durden, an aerial fish spotter who worked with the basking shark fishery during the 1948-1950 period, were published by Squire (1967). These records indicate that basking sharks are commonly observed during October to May, with commercial concentrations noted off Pismo Beach and in Monterey Bay. This occurrence differs from that reported in north European waters where basking sharks are commonly observed during the summer.

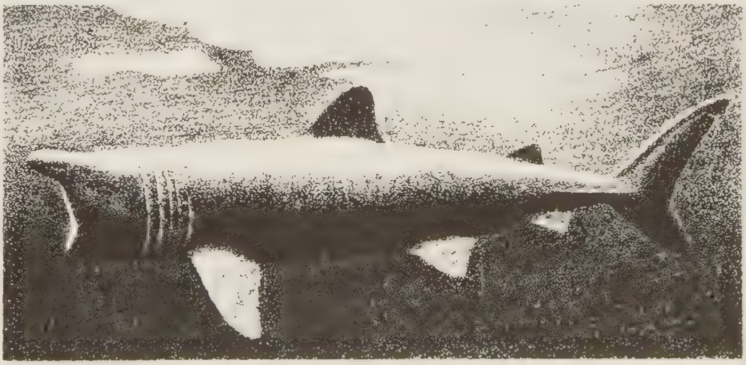
In European waters it is proposed that they may shed their gill rakers in early winter, and hibernate near the bottom during the winter and spring months (Matthews, 1962). Along the California coast, they are frequently observed in areas of high phytoplankton abundance.

In February 1955, the author recorded their occurrence in Monterey Bay during an aerial survey for pelagic fish (Anonymous, 1955). Seventy-four basking sharks were counted in the northeast portion of Monterey Bay, within 1.5 miles of shore. They appeared to be feeding in an area of patchy plankton.

This paper describes the distribution and abundance of basking sharks along the central and southern California coast (1962-85) as recorded by aerial fish spotters participating in the NMFS aerial monitoring program for coastal pelagic resources. Comparison is made of the seasonal occurrence of phytoplankton off the central California coast and the abundance of basking sharks.

Methods

In 1962, the National Marine Fisheries Service Southwest Fisheries Center (SWFC) started an aerial monitoring program for pelagic fish resources using the



The basking shark, *Cetorhinus maximus*.

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services of aerial fish spotter pilots that work with the California commercial purse seine fleet. The spotter pilots search the offshore areas from off Baja California, Mexico, to the Monterey Bay area for concentrations of such target species as the northern anchovy, *Engraulis mordax*; Pacific or chub mackerel, *Scomber japonicus*; jack mackerel, *Trachurus symmetricus*; Pacific bonito, *Sarda chiliensis*; Pacific sardine, *Sardinops sagax*; and bluefin tuna, *Thunnus thynnus*. For the resource monitoring program the spotter pilots maintain a flight log indicating areas searched, species observed, and amount of fish observed (estimated in short tons) for the area, or numbers of schools and size (tonnage) of the schools. Aerial spotters under contract were also asked to make note of any basking sharks observed.

Aerial fish spotting records (1962-85) in the SWFC data base were searched for basking shark sightings. Data on numbers sighted are recorded by "block area," a 10' longitude by 10' latitude area (about 8 × 10 n.mi. at the latitude of California). This "block area" coding system is the same as that used by the California Department of Fish and Game for recording data from the marine waters off California. When a pilot enters a block area it is recorded as a block area flight (BAF). During 1962-85, aerial spotters recorded a total of 6,695 BAF's for the area north of Point Conception (Zones A and B) and 74,142 BAF's for the area south of Point Conception (Zones C and D). During 1962-85, 8,713 basking shark sightings were recorded, distributed along the coast from immediately south of Santa Cruz, California to off Port Hueneme, California, and along the Santa Barbara Channel Islands. Four basking sharks were recorded off northwest Baja California, Mexico.

Results

Figure 1 presents the geographical distribution of sightings, the total number of basking sharks sighted and average number sighted per sighting by block area during 1962-85. The area north of Point Conception, Monterey Bay (block areas 508, 516, 517) and the area off Point Buchon and Morro Bay (block areas 607, 615) had the greatest number of basking shark sightings. Block area 607 had the largest sighting record, 6,389 basking sharks, with an average of 96.8 sharks per sighting. South of Point Conception the greatest number sighted in any block area was the area southwest of Ventura (block 665) with an average of 6.7 individuals per sighting. In this area, block areas 664 and 683 had higher sighting rates, but few sightings (two for block 664 and one for block 683).

The monthly distribution of basking shark sightings for the coastal area from the Santa Barbara Channel to Monterey Bay as developed by the aerial monitoring program (1962-85) is compared with the monthly sightings in the Monterey Bay area as recorded by Edward Durden (Squire, 1967) in 1948-50 (Fig. 2). Both sets of observation data show the peak apparent abundance to be October with a lesser occurrence in February or March.

The Monterey Bay and central California coast is a major upwelling area and the highest phytoplankton concentrations are noted during the summer months. Figure 2 also shows the monthly distribution of phytoplankton volumes in the Monterey Bay area as recorded by Bolin and Abbott (1963). Zooplankton organisms, being grazers on phytoplankton, tend to coexist with phytoplankton, and the months of high phytoplankton should result in higher levels of zooplankton, the major food source for filter-feeding basking sharks. During the months of high phytoplankton volumes the occurrence of basking sharks is low. This may indicate that the basking sharks observed in greater numbers during the fall and winter are not necessarily in the coastal areas for feeding, but these concentrations in the inshore area could be related to mating as described by Compagno (1984) for the European population.

Abundance Trends

Greater abundance levels were observed prior to 1970. This is reflected in the number of basking sharks sighted per block area (for block areas having sightings) as shown in Figure 3. The distribution of sighting effort (number of BAF's) conducted north and south of Point Conception by year, is also given in Figure 3. The number of flights conducted north of Point Conception in the areas of higher basking shark abundance was much greater before 1970 than after. Aerial fish spotters were actively searching for Pacific (chub) and jack mackerel and Pacific sardine north of Point Conception in the 1960's, but after the decline of both the mackerel and sardine resources to very low levels, little aerial spotting effort was conducted north of Point Conception. Edward Durden (personal commun.) reported that from his experience it appeared that the abundance of basking sharks was much reduced in all areas in the 1970's.

A total of 399 sightings totaling 8,709 basking sharks were recorded for the coastal area from Port Hueneme to Santa Cruz, Calif. This was an average of 21.8 basking sharks per sighting. The average number was 51.9 basking sharks per sighting for the area north of Point Conception; for south of Point Conception the average number of basking sharks per sighting was 2.9. South of Point Conception the sighting level was 0.009 basking sharks per BAF (74,143 BAF). North of Point Conception the sighting level was 1.19 basking sharks per BAF (6,695 BAF).

It would appear that some increase in population levels of basking sharks south of Point Conception may have occurred since 1975 with a peak in 1981 (Fig. 3). Severe El Niño perturbations occurred in 1982 and 1983 (Quinn et al., 1987). These abnormally warm years, including 1984 which was warmer off southern California than during the El Niño period, may have reduced again the availability of basking sharks south of Point Conception.

Historical experience in other areas of the world indicates that basking sharks cannot sustain a prolonged intensive fishery (FAO, 1984). Basking sharks, like many other elasmobranchs, have a slow growth rate and low fecundity (Holden, 1973). Fisheries in other parts of the world tend to sporadically fish the elasmobranch resource, as their abundance evidently declines rapidly during fishing (Compagno, 1984). Abundance surveys of the California basking shark resource

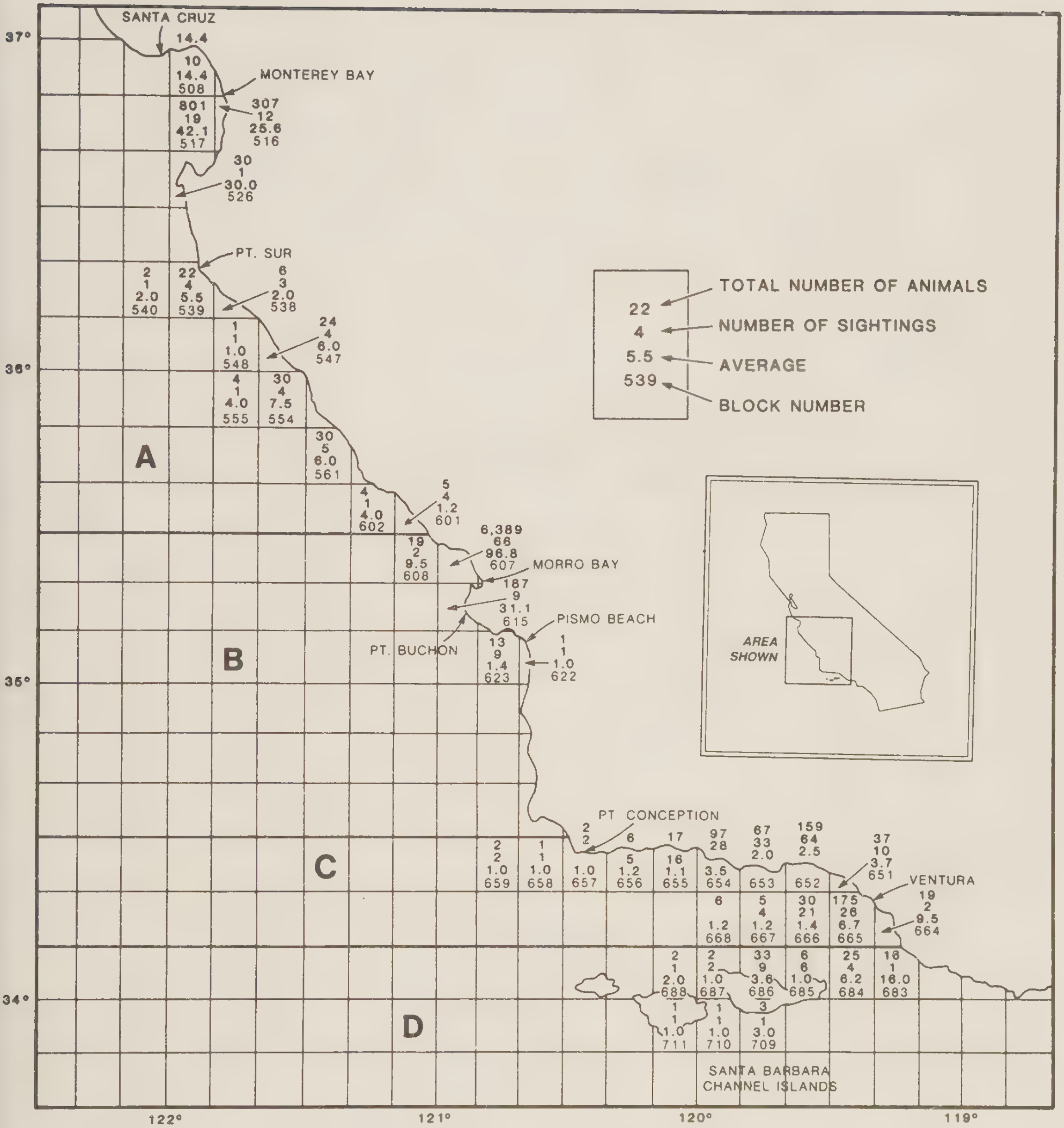
SANTA CRUZ
MONTEREY BAY
PT. SUR
MORRO BAY
PT. BUCHON
PISMO BEACH
PT CONCEPTION
VENTURA
SANTA BARBARA CHANNEL ISLANDS
A
B
C
D
37°
36°
35°
34°
122°
121°
120°
119°
22
4
5.5
539
TOTAL NUMBER OF ANIMALS
NUMBER OF SIGHTINGS
AVERAGE
BLOCK NUMBER
AREA SHOWN
14.4
10 14.4 508
801 19 42.1 517
307 12 25.6 516
30 1 30.0 526
2 1 2.0 540
22 4 5.5 539
6 3 2.0 538
1 1 1.0 548
24 4 6.0 547
4 1 4.0 555
30 4 7.5 554
30 5 6.0 561
4 1 4.0 602
5 4 1.2 601
19 2 9.5 608
6,389 66 96.8 607
187 9 31.1 615
13 9 1.4 623
1 1 1.0 622
2 2 1.0 659
1 1 1.0 658
2 2 1.0 657
6 5 1.2 656
17 16 1.1 655
97 28 3.5 654
67 33 2.0 653
159 64 2.5 652
37 10 3.7 651
6 1.2 668
5 4 1.2 667
30 21 1.4 666
175 26 6.7 665
19 2 9.5 664
2 1 2.0 688
2 2 1.0 687
33 9 3.6 686
6 6 1.0 685
25 4 6.2 684
16 1 16.0 683
1 1 1.0 711
1 1 1.0 710
3 1 3.0 709

Figure 1.—Distribution of sightings, total number of basking sharks sighted, and average number sighted per sighting by block area (1962-85).

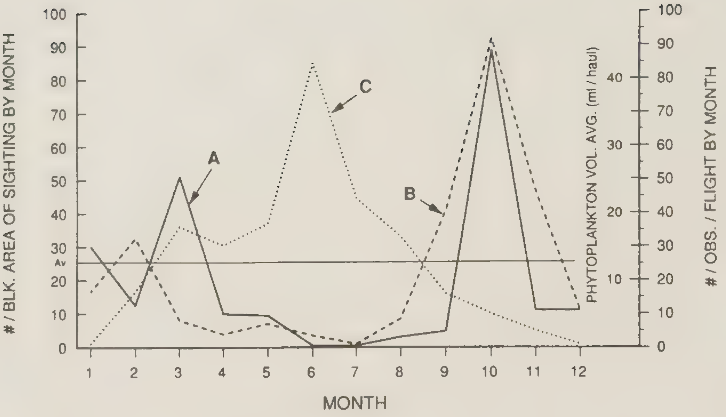

Figure 2.—A = average number of basking sharks sighted per block area, by month, by the aerial monitoring program (1961-85), B = number of basking sharks observed per flight in the Monterey Bay area, by month (1948-50), and C = average phytoplankton volumes recorded for Monterey Bay, by month (1954-60).

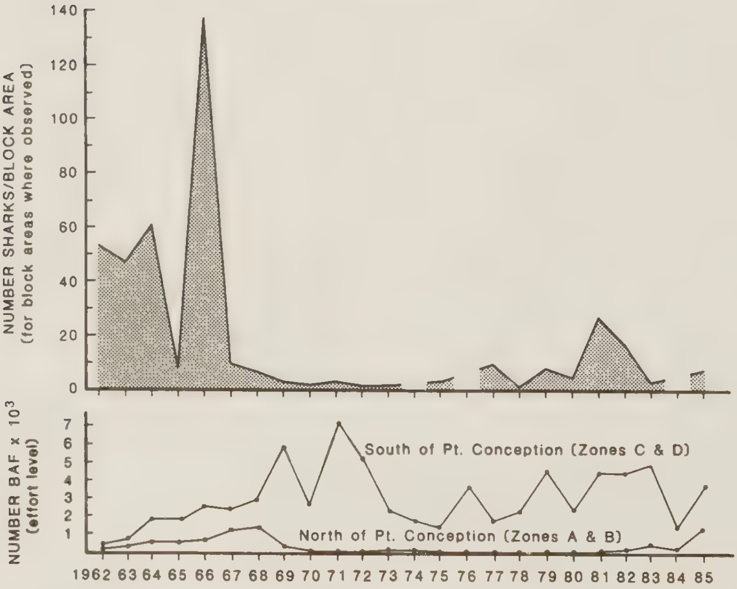

Figure 3.—Number of sharks per block area, for block areas where observed, and number of block area flights (BAF's) north and south of Point Conception, Calif.

should be conducted to establish a "base level" of apparent abundance prior to any commercial fishing, and compared with the historical abundance levels presented here. Continuing the survey program to monitor changes in apparent abundance from fishing would then provide necessary information for resource management.

Literature Cited

Anonymous. 1955. Aircraft spotting flight 55-2. Calif. Dep. Fish Game, Memo. Rep., 4 p.

________. 1956. Ship spears shark. Pop. Mech. 1956(11):172-173.

Bolin, R. L., D. P. Abbott. 1963. Studies on the marine climate and phytoplankton of the central coast area of California, 1954-1960. Calif. Coop. Oceanic Invest. Rep. 9:23-45.

Compagno, L. J. V. 1984. Sharks of the world. FAO Fish. Synop. 125, FAO Species Cat. 4, pt. 1, 249 p. Food Agric. Organ. U.N., Rome.

Holden, M. J. 1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapp. P.-V. Reun. Cons. Int. Explor. Mer. 164: 360-367.

Matthews, L. H. 1962. The shark that hibernates. New Sci. 13:756-759.

Quinn, W. H., V. T. Neal, and S. E. Antunez de Mayolo. 1987. El Niño occurrences over the past four and a half centuries. J. Geophys. Res. 92(C13):14,449-14,461.

Roedel. P. M., and W. Ripley. 1950. California sharks and rays. Calif. Dep. Fish Game, Fish. Bull. 75, 88 p.

Squire, J. L., Jr. 1967. Observations of basking sharks and great white sharks in Monterey Bay, 1948-50. Copeia 1967(1):247-250.

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Striped Marlin in the Northeast Pacific — A Case for Local Depletion and Core Area Management

J.L. Squire and D.W.K. Au

Commercial and recreational fishermen have been fishing billfish along the west coast of the Americas from California to Chile for several decades. Game-fish fishermen using rod-and-reel have fished for sailfish *(Istiophorus platypterus)* in major catch areas off Mexico, Costa Rica, and Panama; for blue marlin *(Makaira nigricans)* and black marlin *(Makaira indica)* off Panama, Ecuador, and Peru; and for striped marlin *(Tetrapturus audax)* off southern California USA, Baja California Sur-Mexico, and Ecuador. There are also commercial harpoon fisheries for swordfish *(Xiphias gladius)* off southern California and Chile and hook-and-line fisheries for marlin and sailfish at localities along the east coasts of the Pacific Ocean. Since 1980, a commercial offshore drift-gill-net fishery has expanded off California, increasing the catches of swordfish and incidentally-caught striped marlin. These are localized fisheries that are dwarfed by Japanese longline operations in the eastern Pacific that began after 1960.

This paper reviews the development of the eastern Pacific longline fishery for striped marlin and its impacts upon recreational fishing. It presents some arguments for "core area" management of the striped marlin resource for providing a suitable level of catch necessary for both longline and recreational rod-and-reel fisheries.

Eastern Pacific Billfish Fisheries

Commercial Fishery

After World War II, the Japanese expanded their longline fishing operations from the western Pacific into the southwest and central Pacific. They began exploration into the eastern Pacific (east of 130°W) in 1956 and, by 1963, were fishing over most of the tropical and subtropical areas of that area (Fig. 1). During this same period, Japanese exploration and longline fishing for tunas and billfishes had also expanded into the Atlantic and Indian oceans.

In 1963, the Japanese shifted considerable longline effort into the northeast tropical Pacific (north to 27°N lat.), where they had already found concentrations of striped marlin, sailfish,

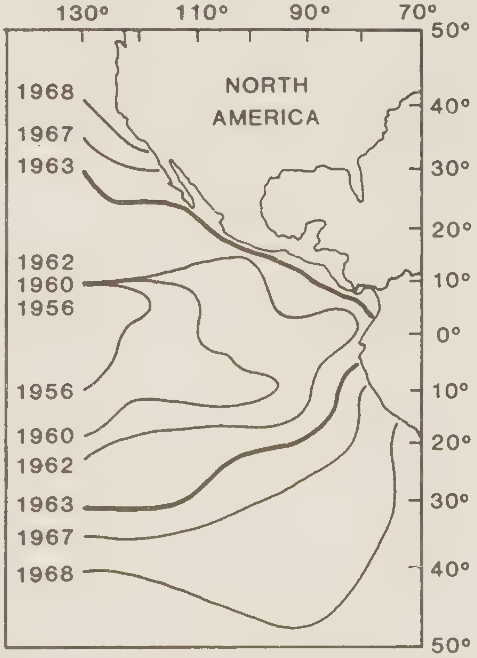

Figure 1. The 1956-1968 expansion of the Japanese longline operations into the eastern Pacific (E of 130°W), adapted from Joseph, Klawe, and Orange, 1974.

and swordfish as well as minor amounts of blue marlin and black marlin. Billfish catches increased in the eastern Pacific (Fig. 2), with the fleet concentrating on sailfish in areas from southern Mexico to Panama and on striped marlin and swordfish in an area from the Clarion and Socorro Islands to the southwestern coast of Baja California Sur, and the lower mouth of the Gulf of California. During 1962-1980, the catch of tunas and billfishes in the eastern Pacific amounted to 23.8 million fish, of which approximately 69% were tunas and 31% billfishes.

Fishery statistics of this expansion into the eastern Pacific have been collected by the Japan Fisheries Agency, which requires that all Japanese longliners prepare daily fishing logs. The results are published annually and give the total species catches and hook effort by 5° longitude and latitude intervals (Anon 1962-1980). Unfortunatly, the Japan Fishery Agency has not released these detailed catch-and-effort data for the years since 1980.

Striped marlin, swordfish, and sailfish catch trends in the Japanese longline fishery are shown in Figure 3 for the period 1956-1980. Striped marlin catches peaked in the eastern Pacific at 338,000 fish in 1968, but have declined since. Swordfish catches increased to 112,000 fish in the late 1960s, then declined by the early 1970s to 28,000 fish, due in part to findings of methylmercury in the fish (the "mercury problem"). Sailfish catches rose rapidly to 417,000 fish in 1965, but declined to 19,000 fish by 1980.

The catches noted preceding are less than the true totals by the amounts caught by Korean and Taiwanese longliners, tuna purse seiners (incidental catch), recreational anglers fishing from Peru to California, and by the commercial swordfish fleet. Some of these fisheries are expanding. The new drift-gill-net fishery off California landed over 25,000 swordfish in 1986, well above the 1978-1980 annual average of 4,500 fish taken by the traditional harpoon fishery.

Even so, the Japanese longline fleet and its associated joint-venture operations still comprise the major fishery for billfish in the eastern Pacific. Moreover, it is the only oceanic longline fishery there that has maintained acceptable fishing records over a long period of time.

Rereational Fishery

The billfish catch in the eastern Pacific taken otherwise than by longline is relatively minor. The recreational catch of striped marlin off California takes about 800 fish per year. [In contrast, an estimated 1,500 other striped marlin have been taken incidentally there in recent years

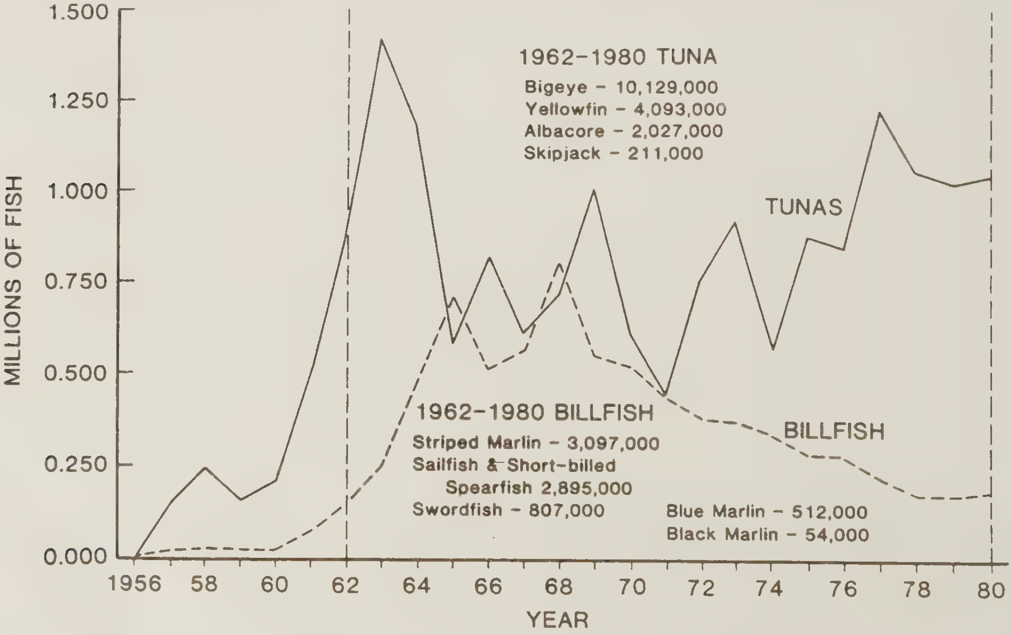

Figure 2. Catch by year for billfish and tuna, 1956-1980, by Japanese longline east of 130°W.

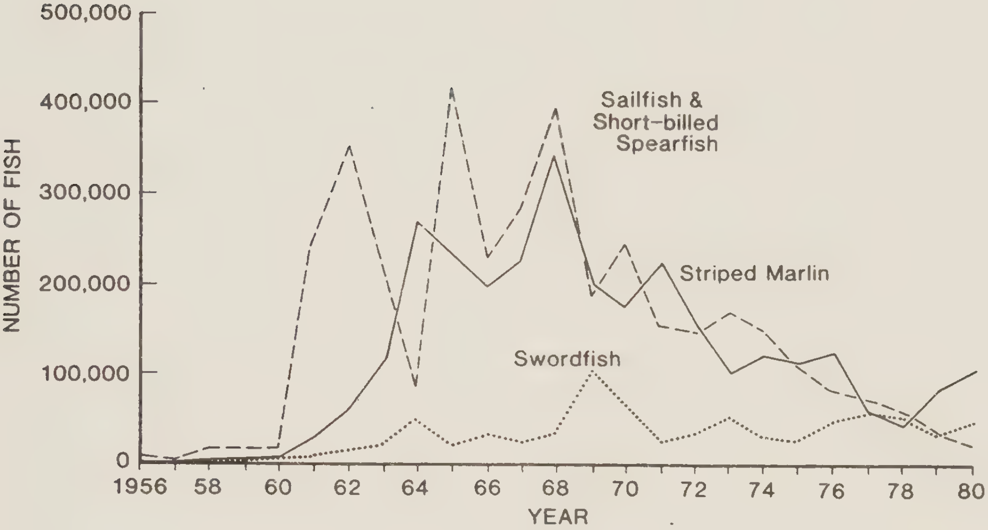

Figure 3. Eastern Pacific Japanese longline catch of sailfish and short-billed spearfish, swordfish, and striped marlin.

by the drift-gill-net fishery for swordfish and thresher shark (*Alopias* sp.).] A preliminary estimate of the recreational catch off Mexico (Joseph, unpubl. MS[1]) indicated 40,000 to 90,000 billfish taken per year. Most are Pacific sailfish, high production areas of which occur off Acapulco, Zihuatanejo, and northward to Mazatlán. The estimated annual Mexican recreational catch of striped marlin is 7,000 to 15,000 fish, the majority from around the southern tip of Baja California Sur. High angler catch rates for striped marlin (0.4 or more fish per angler day), plus occasional catches of blue marlin and black marlin, attract anglers to that area from the United States and many other countries.

Commercial companies that service recreational anglers are very important to the economy of the southern tip of Baja California, and catch rates must meet anglers' expectations. Recently, operators from the major sport fishing locations there have complained of declines in billfish catches, which they have blamed on newly developed, joint-venture longline fisheries.

The Striped Marlin Fishery

Management Approaches

Although Pacific-wide management of pelagic billfishes has long been considered, it is unrealistic to expect such management in the near future. The only international agency that has investigated management for billfish on an ocean-wide basis is the International Commission for the Conservation of Atlantic Tunas (ICCAT). That organization was formed before the widespread adoption of 200-mile economic or fishery zones in most areas of the world. The recent adoption of such by many Pacific countries complicates development of a single multilateral international agency for the Pacific.

Countries having substantial catches of billfishes and high catch-per-unit effort (CPUE) rates within their 200-mile zones readily foresee that localized restrictions upon foreign fishermen can have a measurable impact upon their own billfish fisheries. Economic conflicts among different billfish fisheries within these countries' extended boundaries also heighten the incentive for management. Interest in management of a pelagic resource at a localized level thus gains momentum.

The striped marlin resource around the southern tip of Baja California, Mexico, constitutes such a fishery. It supports a very productive localized commercial longline fishery having the highest reported CPUE in the Pacific. It also supports an economically important and productive recreational billfish fishery. Localized management that is restricted to this "core area" of striped marlin distribution (core-area management), and which provides for both fisheries, would thus appear feasible. Demonstrations of area depletion (or local depletion) of stock as grounds for this kind of management must, however, be viewed within the context of the entire exploited stock.

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[1] Joseph, J. 1981. Report on the development of a Mexican longline fishery, unpublished.

Management actually began in 1976 when the government of Mexico proclaimed a 200-mile exclusive economic zone (EEZ). In early 1977, Mexico made a concerted effort to enforce its conditions. Japanese and U.S. longliners, as well as other foreign nationals operating within the 200-mile limit, were not allowed to continue fishing. In 1980, however, a number of permits were issued, thereby allowing the operation of several foreign longliners in a joint-venture program within the EEZ. Commercial longlining under permit continued until mid-1984, when permits were again withheld. Permits were reissued in late 1985, and it is reported (M. Comparan, pers. comm.) that approximately 14 longliners were operating under permit in 1987, targeting on striped marlin and swordfish (plus 6 shark longliners which catch striped marlin incidentally). *[NB:* On many of our graphics, we show a dashed line separating the years 1977 to 1980 and 1984 to 1985, indicating the times during which there was enforcement of Mexico's 200-nautical-mile economic zone, when no longline permits were issued.] In August 1987, following strong complaints by sport fishing operators, new regulations were issued that restricted these longline operations to the offshore areas of Mexico's 200-mile zone, out of the high-catch-rate areas.

For slightly over 3 years — the first period when permits were withheld (early 1977 to late 1980) — commercial longlining was nearly nonexistent in that area having the highest striped marlin catch rate in the Pacific (see following) and also a high catch rate for swordfish. It is rare in the annals of high-seas pelagic fishing that a major catch area, or core area of abundance, becomes restricted, bringing catches nearly to zero. Although not designed as such, the government of Mexico had conducted an "experiment" that showed how a widespread offshore fishery affects local fishing.

Catch, Effort, and CPUE

The longline fishery. In the eastern Pacific (E of 130°W) the hook-effort generated by the longline fishery fluctuated but increased after 1961 in three stages: a sharp increase in the early 1960s, a moderate increase from 1964 to 1974, and a greater increase since then (Fig. 4) — from about 62.0 million hooks fished in 1964, to a 102.5 million hook-effort in 1980 (the latest data available).

The CPUE for catches of tunas and billfishes (all species) (Fig. 5) reflects a decline in tuna CPUE prior to the increased emphasis on billfish fishing in 1964.

The longline catch of striped marlin is incidental to the catch of tunas in most areas of the eastern Pacific. There are greater than average catches off Mexico, however, around and south of the Galapagos Islands, and in an area about 400 miles west of Peru during the southern summer (northern winter). Off Mexico, striped marlin and swordfish are notably targeted because of high CPUE rates. The best fishing areas are within the 200-mile economic zone. About 40% of the striped marlin catch (by weight) in the eastern Pacific is generated off Mexico (Joseph, unpubl. MS[1]).

The longline catch of striped marlin in the eastern tropical Pacific increased sharply to 270,000 fish in 1964 (Fig. 3), much of it from increased hook-effort off Mexico. The catch peaked again in 1968 at 338,000 fish, and then declined to 130,000 fish in 1976. As mentioned previously, these Japanese billfish catches are short of the total catch by the amounts of the recreational catch and incidental and directed catches by other fishing fleets. Unfortunately, neither these other catches nor the associated fishing effort are well documented.

Longline catch records show that the geographical area from off Magdalena Bay (on the southwest coast of Baja California) to the Clarion and Socorro Islands, and to the southern portion of the Gulf of California, has the highest catch rates in the Pacific (Suzuki and Honma 1977[2]). The Japanese records (Anon 1962-1980) of catch and hook-effort by 5° longitude and latitude areas show that two areas, 20°N by 110°W and 20° by 105°W (long. and lat. of lower right-hand corner of each 5° area), constitute the most important longline fishing locality for striped marlin in the Pacific (Fig. 7). These two 5° areas, or core areas of striped marlin abundance, accounted for about 23% of the total catch by number of striped marlin in the eastern Pacific (E of 130°W) prior to the establishment

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[2] Suzuki, Z. and M. Honma. Stock assessment of billfishes in the Pacific. Working paper, Billfish Stock Assessment Workshop, Honolulu, HI, 5-16 Dec. 1977, unpublished.

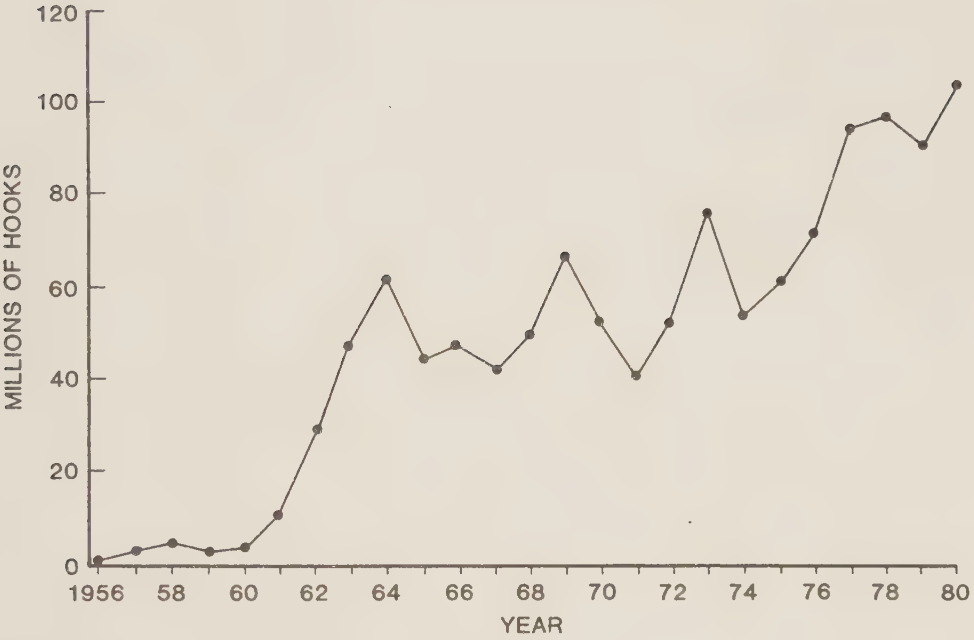

Figure 4. Longline hook effort (Japanese) east of 130°W.

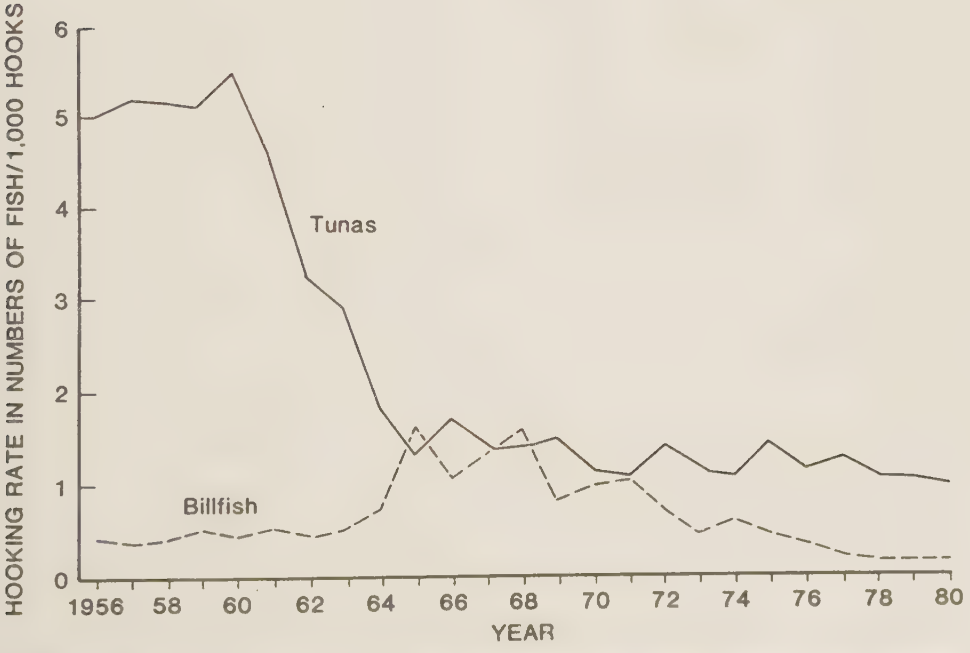

Figure 5. Catch rate for Japanese longline, tunas and billfish in the eastern Pacific in numbers of fish/1,000 hooks.

of the Mexican 200-mile limit.

The recreational fishery. In 1969, the National Marine Fisheries Service started the Pacific Billfish Angler Survey (Squire 1987a, 1987b). This annual survey collects catch-and-effort data from rod-and-reel billfish anglers. From these data, a CPUE (catch-per-unit-effort and/or number of fish per angler-day) is computed for the major recreational billfish fishing areas. Trends in the recreational striped marlin CPUE (1962-1980) for the above two 5° areas about the southern tip of Baja California. Mexico are southern tip of Baja California, Mexico, are shown in Figure 6. The trend of both the commercial longline and recreational fishery CPUE was downward prior to 1977. The commercial longline fishery declined at an average annual rate of about 0.90 fish per 1,000 hooks fished per year, or 5% per year. The recreational catch declined at a rate of about 0.04 fish per angler-day per year, or 6% per year.

Relationship Between the Fisheries

Re CPUE trends. The relationship between the inshore recreational fishery, the offshore joint-venture longline fishery (within Mexico's 200-mile limit), and the longline fishery in the remainder of the eastern Pacific, must be considered in any management plan. Figure 6 shows

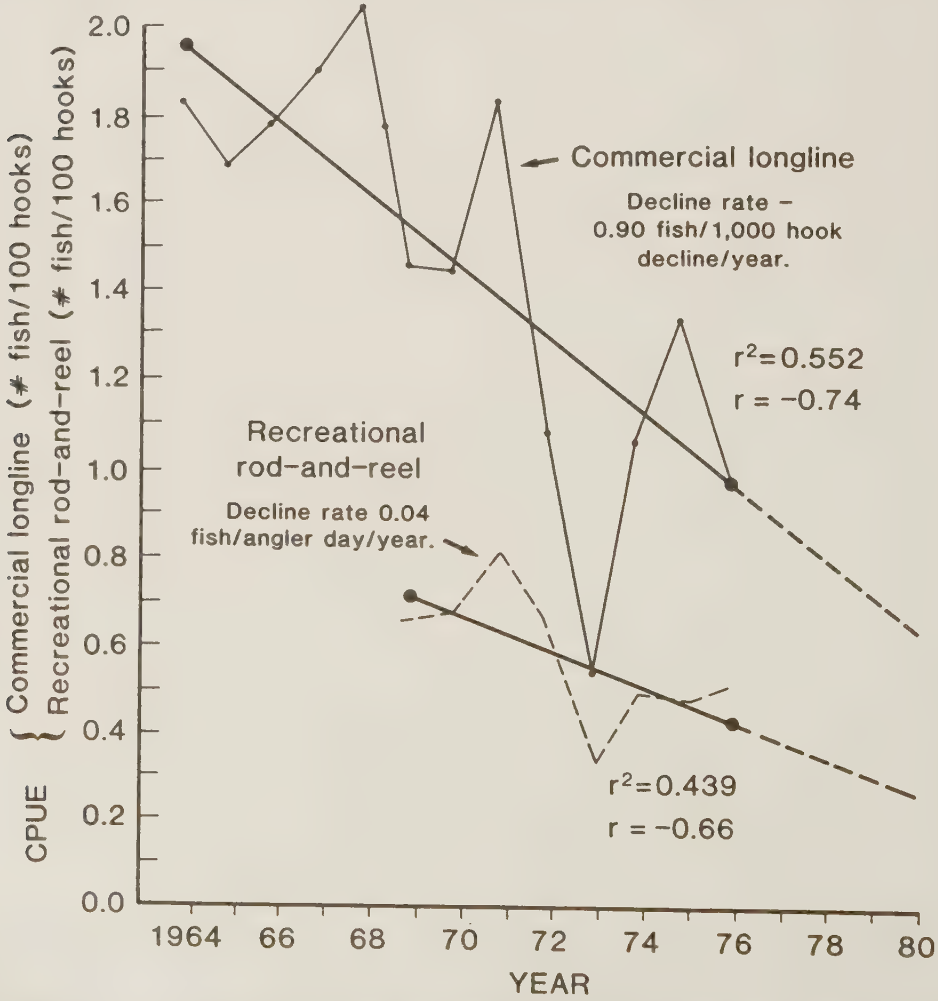

Figure 6. Catch rate and regressions for commercial longline in 5° long. by lat. area (20°N × 105°W) and for the recreational rod-and-reel fishery about the southern tip of Baja California, Mexico.

an apparent correlation between the CPUE trend of the recreational fishery and that of the commercial longline fleet operating near the southern tip of Baja California. This is better shown in Figure 10 which also shows the correlation during the years 1980 through 1986. These correlations, between commercial and recreational CPUEs (data normalized), are statistically significant ($r = 0.89$, 0.96; $Ps < 0.01$). There is a further close relationship between the population in the two 5° longitude by latitude, high CPUE areas off Baja California (20°N × 110°W), and that of the remainder of the eastern Pacific, as indicated by similarity in the respective CPUE fluctuations (Fig. 7). It is therefore reasonable to assume that the CPUEs generated by the longline fleet off Baja California are generally representative of the total eastern population.

Re movements. Examination of data representing over 12,000 striped marlin tagged by anglers in the northeast Pacific (mostly tagged near the tip of Baja California) suggests an interchange of fish between waters off southern Baja California and surrounding areas. There appears to be movement from the southern tip of Baja California to the south and southwest in early summer, and also some movement to the northwest (Squire 1987b). There were few long-distance and few long-term (>2 years) recoveries. Most recoveries were at distances relatively near the area of tagging. Figure 8 shows the average recapture distance from the major locations of tagging off Baja California and Mazatlán for various release-recapture periods. These data suggest that fish move outward from the high-catch areas to the surrounding low-catch-rate oceanic areas. The reasons for this movement are not well known but may be related to movements to major spawning areas (Squire and Suzuki 1989), or to seasonal changes in desirability of the area.

Similarly, an analysis of the movements by striped marlin from important longline fishing areas in the eastern Pacific (Squire and Suzuki 1989), from CPUE data provided by Suzuki and Honma (1977)[2], indicated a south and southeast seasonal movement of the resource. This movement resulted in increased catch rates in the central-eastern and southeastern Pacific during the northern winter (southern summer). A northwestward movement to areas of higher longline CPUE was also evident in the northern spring and early summer.

Re morphometrics. Measurements of striped marlin lengths (eye orbit to fork of tail) in the eastern Pacific (Suzuki and Honma 1977[2]) suggest a pattern which may reflect long-term

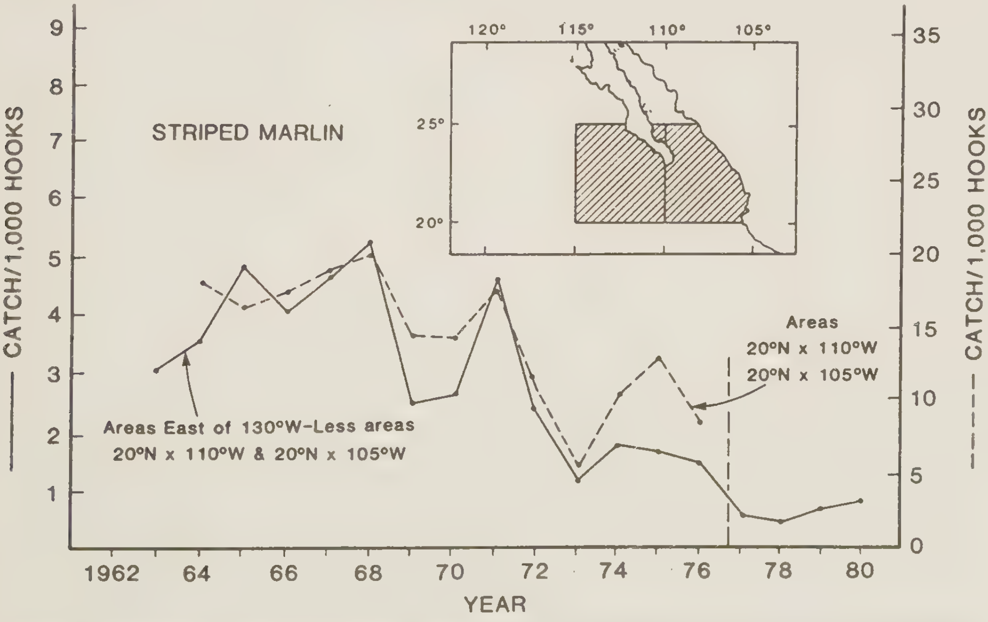

Figure 7. Comparison of CPUE's for the total eastern Pacific (E of 130°W) less 2-5° long. by lat. areas about Baja California and the CPUE for the 2-5° areas combined.

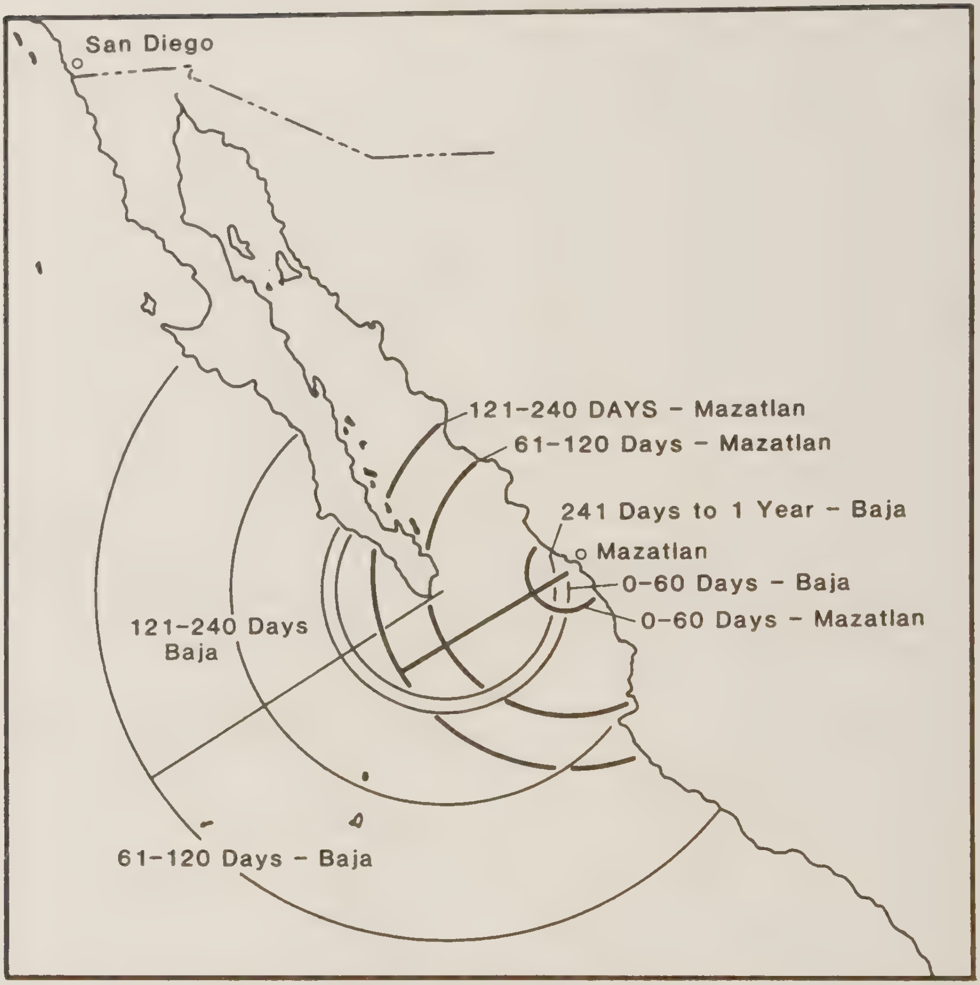

Figure 8. Migration distances by time periods from tagging to recovery, 0-60, 61-120, 121-240, 241 days to 1 year for tagging off Baja California and Mazatlán, Mexico.

fish movements. The marlin in the northeast Pacific are slightly smaller (in mode) than those in the southeast Pacific. There appears to be a cline in the length-frequency pattern from the north-central Pacific to the northwest, northeast, southeast, and southwest Pacific (Squire and Suzuki 1989). Samples from the recreational striped marlin catch off Baja California, Mexico, indicate that the average eye-fork length is about 160 cm (Wares and Sakagawa 1974). This length compares favorably with the historical length-frequency data for the longline fishery off Mexico (Suzuki and Honma 1977[2]) and with length measurements collected recently by the Mexican-Japanese joint-venture fishery from the port of Ensenada, Mexico (Squire; pers. comm., M. Comparan). These areal changes in length frequency suggest that the fish move toward the eastern Pacific and southern Baja California as they grow. These findings suggest that the high-catch-rate areas off Mexico are areas of at least temporary accumulation or aggregation for fish of about 160-170 cm in eye-fork length. Individuals longer than 210 cm do not appear to remain in this area in any number. Movements of the larger fish may be related to maturity and, thus, to spawning seasons and spawning areas.

Local CPUE Changes off Mexico

Billfish angler survey trends. Striped marlin catch rates, determined from the Pacific Billfish Angler Survey (catch per angler-day), are shown in Figure 9. Additionally, and prior to the start of the Angler Survey in 1969, logbook data had been made available by Rancho Buena Vista, an important fishing resort on the East Cape area of Baja California. These records indicated a catch rate (fish per angler-day) of 0.60 for 1965, 0.73 for 1967, and 0.90 for 1968. The Angler Survey then showed a declining CPUE trend for Baja California, 1969 through 1976 (Fig. 9). This trend then reversed, and CPUEs increased in 1978, 1979, and 1980. Since 1980, CPUEs in the Baja California sport fishery have fluctuated at about 0.5 fish per angler-day. The nearby southern California rod-and-reel fishery, which has consistently shown a low CPUE (about 0.1 fish/day), showed little trend. The catch rate increased slightly after 1981, and the highest catch rate recorded was in 1985, slightly over 0.3 fish per day. It returned to the 0.1 CPUE rate in 1986.

The cited changes in angler CPUE reflect similar changes in longline CPUE in adjacent oceanic areas, as previously noted. This situation (Fig. 10) is a composite of, (a) longline CPUE in the eastern Pacific excluding the two 5° longitude by 5° latitude areas about the tip of Baja California (20°N × 105°W and 20°N × 110°W); (b) longline CPUE in the two excluded 5° longitude by latitude areas only; and (c) CPUE from the recreational striped marlin fishery about the tip of Baja California. Examination of the figure indicates the following trends of longline CPUE change as affected by fishery closures.

In the Japanese longline fishery. Total eastern Pacific catch-and-effort data — less data for the two 5° areas off Baja California — show a decline in CPUE from 1964 to 1978, from about 5 to 0.4 fish per 1,000 hooks (nominal effort) fished, with a decline rate of 0.38 fish per 1,000 hooks fished per year. Since the early 1970s, considerable deep-longlining has been conducted in the equatorial area for bigeye tuna *(Thunnus obesus)*. This method of longlining reduces the chances of catching billfish. For the two 5° longitude by latitude areas off Baja California — where bigeye tuna fishing is relatively unimportant — the CPUEs declined during the period 1964 to 1976 from about 18 to 9 fish per 1,000 hooks fished, with a decline rate of 1.10 fish per 1,000 hooks fished per year. Then, during the period of restricted fishing, 1979 and 1980, the CPUE rose to near 23 fish per 1,000 hooks fished for both years. [Japanese longline catches within the two 5° areas that are within Mexico's 200-mile economic zone may have been from joint-venture longliners.] After 1980, Japanese longline data were no longer accessible.

In the Mexican joint-venture longline fishery. Sampling of Japanese longliners, operating on a joint-venture arrangement within the 200-mile limit and out of the port of Ensenada, Mexico (courtesy of Comapro SA. de CV.), showed that the CPUE in 1980 had risen to 22.0 fish per 1,000 hooks fished (Table 1). From the spring of 1984 to the fall of 1985, permits to operate

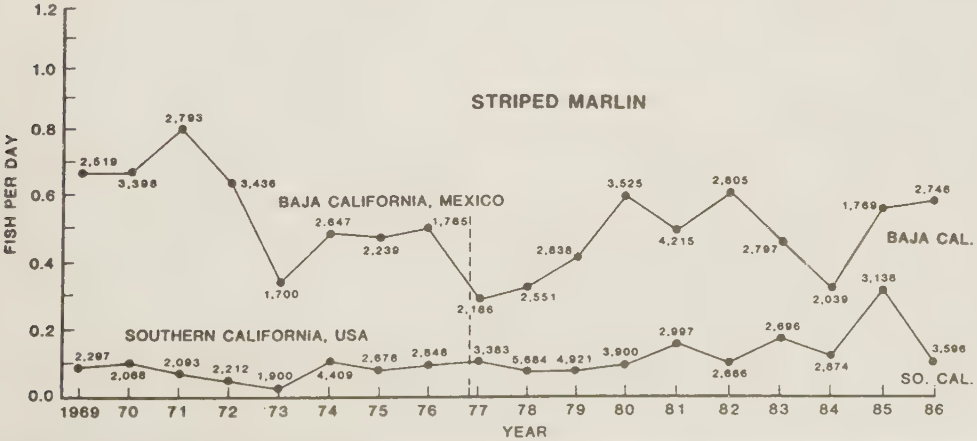

Figure 9. CPUE trend (fish per angler-day) for striped marlin about the southern tip of Baja California, 1969-1985, from the Pacific billfish angler survey. Numbers by the points indicate angler-days.

within Mexico's 200-mile limit were again withheld. During that period, the CPUE rose by about 1.5 fish per 1,000 hooks fished per year.

Table 1. CPUE data obtained from a portion of the joint-venture Japanese fleet operating from Ensenada, Mexico (courtesy Comapro SA. de CV.).

Year	# hooks fished	# fish/1,000 hooks
1980	547.000	22.0
1981	1,899.900	12.0
1982	1,235.000	23.0
1983	178.600	12.0
1985	143.000	16.0
1986	301.300	13.0

The Fishing Areas

Intensive and productive fishing actually occurs in only portions of the approximately 165,000 sq.-n.mi. core area, probably due to environmental conditions (Hanamoto 1974). Figure 11 shows fishing effort distribution for a portion of the joint-venture longline fleet operating in 1982 and 1983. The most productive fishing areas were along the edge of the continental shelf off Magdalena Bay, at the mouth of the Gulf of California, and around the Revillagigedo Islands. Catches were primarily of striped marlin during the summer from off Magdalena Bay to the Revillagigedo Islands, and of both swordfish and striped marlin during the winter months off Magdalena Bay and about the mouth of the Gulf of California.

Summary

Changes in angler-CPUE appear to reflect offshore changes in the exploited population. From 1969 to 1977 (the year after the last full year of unrestricted commercial longline fishing), the angler-CPUE had declined from 0.69 to 0.30 fish per angler day, about 0.04 fish per angler day per year (Fig. 10). During the restricted commercial longlining period from 1977 to 1980, when longline-CPUE increased by about 3.6 fish per thousand hooks per year, the angler-CPUE increased from about 0.3 to 0.6 fish per angler-day. This increase is about 0.15 fish per angler-day per year. Since 1980, when joint-venture longline fishing began, the billfish-angler-CPUE showed a decline, again, from about 0.58 to 0.46 in 1985, a decline rate of 0.02 billfish per angler-day per year. The changing trends in angler-CPUE therefore appear to follow the major changes in the offshore commercial fishery (Fig. 12).

Core-Area Assessment and Management

Concept

Regardless of the status of an oceanic stock, or of any overall management regime implemented, local reductions in CPUE usually precipitate calls for restrictions on fishing. The restrictions are usually aimed at extra-local fisheries, and may be justified if those fisheries control the abundance or availability of fish in the local area. Extra-local management may

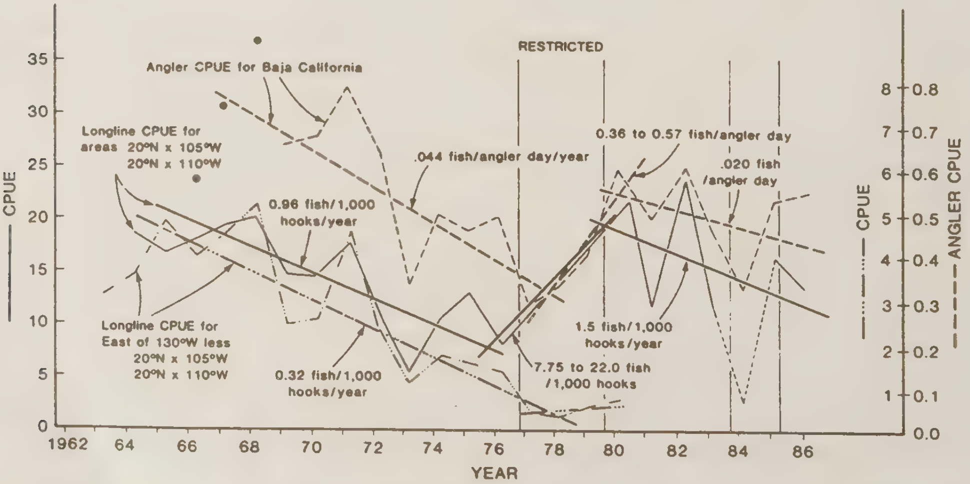

Figure 10. Comparison of CPUE trends for longline in the total eastern Pacific and for rod-and-reel and longline about Baja California.

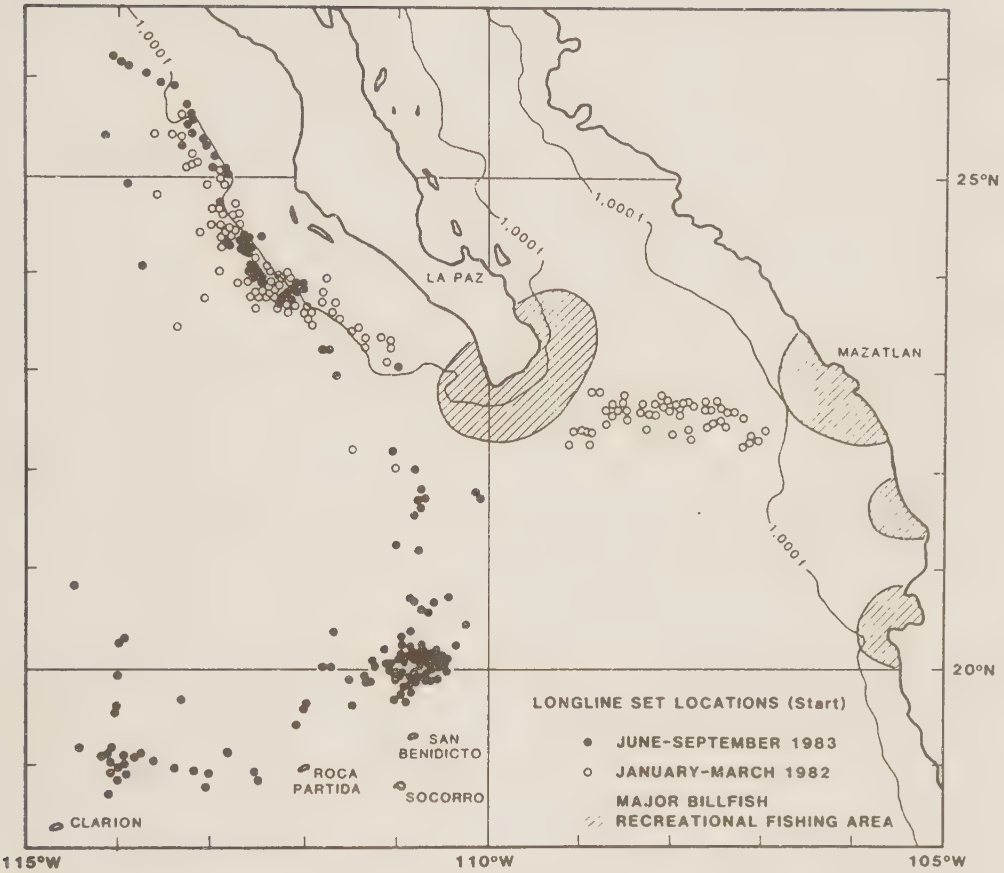
1,000f
1,000f
1,000f
1,000f
25°N
20°N
LA PAZ
MAZATLAN
SAN BENIDICTO
ROCA PARTIDA
SOCORRO
CLARION
LONGLINE SET LOCATIONS (Start)
● JUNE-SEPTEMBER 1983
○ JANUARY-MARCH 1982
▨ MAJOR BILLFISH RECREATIONAL FISHING AREA
115°W
110°W
105°W

Figure 11. Locations of the start of longline sets (portion of joint-venture fleet) during the winter and spring of 1982 and summer of 1983.

itself be restricted in scope, designed only to alleviate the local fishery problem. When the stock concerned is part of an international oceanic fishery, such management requires international agreement or else political control in the relevant areas.

It is preferable, of course, for extra-local management to address the status of the entire stock, but it need not encompass all external fisheries. It may be restricted to certain localized core distribution areas if the stock aggregates toward such areas, or if for any other reason the population there has a controlling relationship to the abundance of the entire stock.

The two 5° latitude × longitude blocks off southern Baja California, Mexico (Fig. 7) can be considered a core area for eastern Pacific striped marlin. Approximately 23% of all striped marlin caught in the eastern Pacific (E of 130°W) comes from that localized area. The evidence presented suggests here that the fish are attracted to, or regularly linger while passing through, that area during their growth and development (see, also, Squire and Suzuki 1989). This core area produces the highest catch rates for striped marlin, and is the focal area for its fishery in the Pacific. Furthermore, the CPUEs in the core area correlate with both the species' CPUEs in the entire eastern Pacific (exclusive of the core area) and with the sport-fishery CPUEs along the Mexico coast (Figs. 6, 7, and 10). The former relationship is due to the attractiveness of the core and surrounding areas to the species — probably for feeding (Hanamoto 1974); the latter relationship is due to the proximity of the core area to the localized shore-based sport fisheries. While these CPUE trends may be correlated, however, the time rates of these CPUE

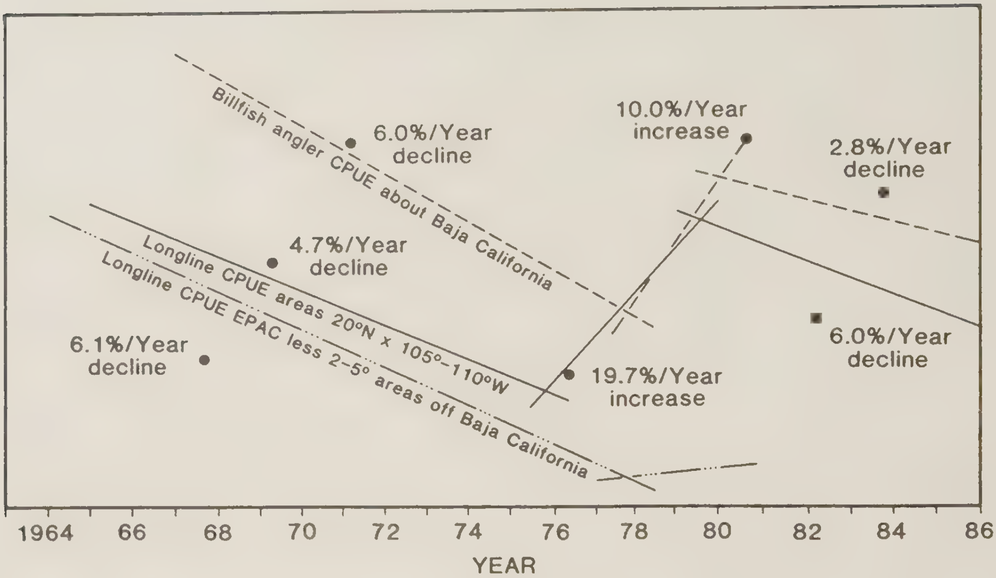

Figure 12. Percentage catch rate change per year for commercial longline and recreational rod-and-reel fisheries.

changes should not necessarily be the same. Each local fishing area is characterized by its own catchability and availability factors and, therefore, by the nature of its response to fishing. The more localized an area, the more likely its CPUE changes will differ from those of other areas.

Mexico's fishing "experiment", which temporarily curtailed the fishery within its 200-mile EEZ, encompassed the core area and showed an effect of fishery interactions. When commercial fishing was stopped, during 1977-1980, the CPUEs rose from a long period of decline to near pre-exploitation levels, both in the core area longline fishery and in the sport fishery (Figs. 10 and 12). These increases all occurred within a 3-year period. Considering the large areal extent of the striped marlin resource, and its overall fishery in the eastern Pacific, together with the limited areal extent of the core and shore-based sport fisheries, this rapid increase in CPUE would appear to reflect effects from the fishing down and rebuilding of localized fishing "hot spots," whose populations are continuously augmented by immigration, rather than overall stock recovery from a decline.

From the foregoing, and evidence previously presented, it is argued that management in the core area off Mexico is feasible (relative to ocean-wide, international management) and can even effect control of the eastern Pacific stock. Moreover, as that stock declines from increased fishing, core-area management could exert even greater control because the percentage of the entire stock attracted to the core area should increase. Since all of the two 5° square areas constituting the core area lie within Mexico's 200-mile EEZ, Mexico has a controlling position to implement core-area management. Such management could endeavor to maintain CPUE levels consistent both with the principles of stock management for the commercial fishery and with needs for an economically viable CPUE level in the adjacent sport fisheries.

Weighted CPUE vs. Fishing Effort

The relationship between striped marlin CPUE and fishing effort was examined using the same Japanese catch-effort data and Mexican-Japanese joint-venture records already described, but here the CPUE was calculated as an area-weighted index (see Beverton and Holt 1957, p. 148). This CPUE was calculated for both an "index" area and for an enlarged core area that consisted of four adjacent 5° square areas (Fig. 13). The index area consisted of 17 whole or partial 5° squares where striped marlin appeared to be the target species in the Japanese fishery. These areas exhibited consistent high catches and catch rates for striped marlin, and

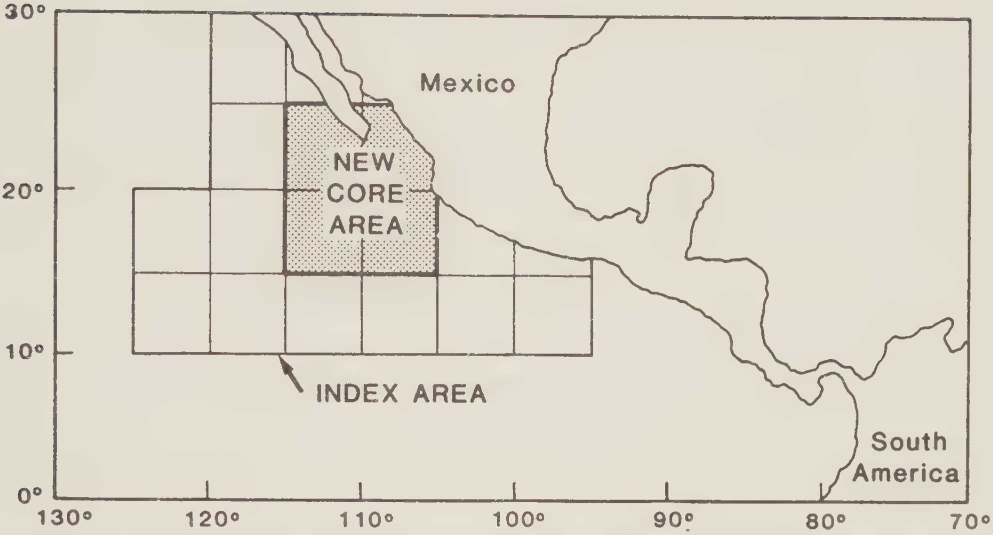

Figure 13. Core and index areas for which CPUEs were calculated as area-weighted averages of CPUEs from each 5° area.

relatively low yellowfin tuna *(Thunnus albacares)* catches. Furthermore, yellowfin tuna catches were greater than bigeye tuna catches, i.e., deep-longlining was not likely to have been important there. The new expanded core area included two adjacent 5° squares directly south of the two squares of the previously described core area. These two new squares are often intensely fished and are significant producers of striped marlin; their inclusion therefore increased the sample size for core-area calculations. In both the index and new core areas, CPUE was calculated only from those 5° squares for which fishing effort, during any time period of interest, was at least 10,000 hooks. This condition was applied to reduce the computing of extreme CPUE ratios.

Results

The time trend in the area-weighted CPUEs (Table 2) was closely similar to that of the simple (effort-weighted) CPUEs previously calculated (Fig. 10). This similarity is an indication of a fishery that is highly focused onto prime fishing areas, i.e., the average catch rate is little altered by inclusion of fishing rates from other areas. In both CPUE series, there was a general decline with time through 1976 or 1977, a rapid rise to near pre-exploitation CPUE levels during the 1977-1980 years of fishery closure, and a decline afterwards in the joint-venture fishery. The area-weighted core- and index-area CPUEs were clearly correlated (since the index-CPUE pertains to a large area that incorporates the new core area). After 1968, the CPUEs declined in a way that indicated the eastern Pacific striped marlin resource had become fully exploited (as seen, also, in Figure 10 for the effort-weighted index).

CPUEs (and also total catches) for the years 1969 to 1984 were therefore plotted against fishing effort to determine their relationship (Fig. 14) in terms of annual index-area CPUE vs. annual effective hooks, the latter calculated by dividing annual catch by annual CPUE. There appears to be a negative regression in the 1969 to 1976 data, although this relationship is obscured if core, not index, area CPUEs are plotted against core hook effort, in turn calculated either from annual or 2nd semestral CPUEs (most striped marlin are taken during the 3rd and 4th quarters of the year).

Reexamining Figure 14, it can be seen that the apparent regression depends strongly upon the 1971 and 1973 data points, which represent good and poor fishing years, respectively (Fig. 10 and Table 2). The more recent data shown cannot be considered very reliable with respect to the stock size-fishing effort relationship. The 1979 and 1980 catch-effort data were sampled from a largely closed near-shore fishery, and the post-1980 data points were based on a tenuous assumption that joint-venture catches were the only catches in the index area. The

Table 2. Catch, catch/effort (CPUE), and effort in the eastern Pacific striped marlin fishery (Japanese and Mexican data only), 1962-1984.

	Annual catch (number of fish)			CPUE (fish per 1,000 hooks)						Annual effective effort (10⁶ hooks) in							
										Japan longline						Mex. JV	
	Jap. LL		Mex JV	Jap. LL				Mex. JV		From index area				From core area		From core area	
				Annual¹		Semester²		Ann.¹	Sem.²	Ann.³	Sem.⁴	Ann.⁵	Sem.⁶	Ann.⁵	Sem.⁶	Ann.⁵	Sem.⁶
Year	Index	Core	Core	Index	Core	Index	Core	Core	Core	CPUE	CPUE	CPUE	CPUE	CPUE	CPUE	CPUE	CPUE
1962	742	—		4.35	—	2.40	—			0.17	0.31	—	—	—	—		
1963	8,796	6,799		17.93	41.80	17.12	39.02			0.49	0.51	0.21	0.22	0.16	0.17		
1964	145,120	125,346		9.44	16.43	10.76	14.94			15.37	13.49	8.83	9.71	7.63	8.39		
1965	103,300	75,781		9.54	14.17	10.72	14.53			10.83	9.64	7.29	7.11	5.35	5.22		
1966	71,268	53,894		10.03	16.16	10.54	17.05			7.10	6.76	4.41	4.18	3.34	3.16		
1967	100,224	78,082		11.12	18.20	12.19	16.98			9.01	8.22	5.51	5.90	4.29	4.60		
1968	220,552	179,623		14.12	19.03	16.25	19.57			15.62	13.35	11.59	11.27	9.44	9.18		
1969	93,713	82,350		11.61	14.28	12.73	13.95			8.07	7.36	6.56	6.72	5.77	5.90		
1970	89,345	82,312		11.23	13.00	11.68	14.31			7.96	7.65	6.87	6.24	6.33	5.75		
1971	114,877	99,730		15.65	16.53	16.09	17.41			7.34	7.14	6.95	6.60	6.03	5.73		
1972	79,176	74,885		9.65	12.49	10.53	12.32			8.20	7.52	6.36	6.43	6.00	6.08		
1973	57,764	53,689		4.63	7.02	5.30	6.61			12.48	10.09	8.23	8.74	7.65	8.12		
1974	76,964	74,151		7.92	10.79	8.18	10.89			9.72	9.41	7.13	7.07	6.87	6.81		
1981			19,024					5.07	14.36							3.75	1.32
1982			11,117					9.22	14.31							1.20	0.78
1983			23,916					6.71	8.34							3.56	2.87
1984			1,992					4.59	1.92							0.43	1.04

[1] Annual values.
[2] 2nd semestral values.
[3] Calculated from index area annual CPUE.
[4] Calculated from index area 2nd semestral CPUE.
[5] Calculated from core area annual CPUE.
[6] Calculated from core area 2nd semestral CPUE.

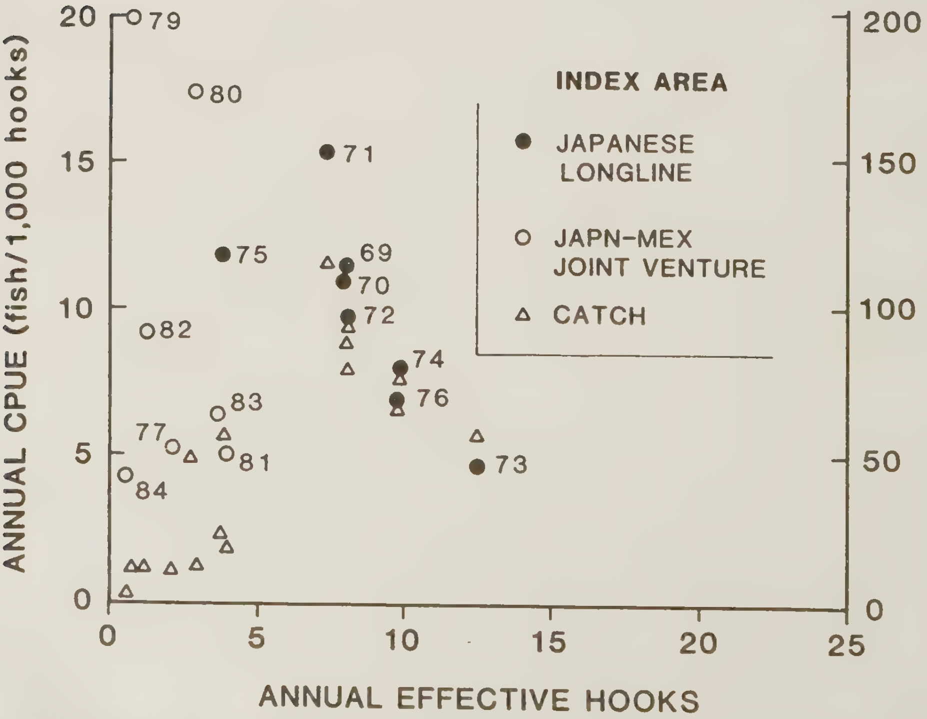

Figure 14. Relationship of index-area annual CPUE and annual catch to annual effective fishing effort. Catch is represented by triangles, annual CPUE by circles.

data appear insufficient to describe the expected negative relationship between CPUE and fishing effort in the eastern Pacific, in spite of the clear time trend of decreasing CPUE off Mexico.

Discussion

The amount of decrease in CPUE that occurred in the core area and elsewhere in the eastern Pacific during the years of active longline fishing was probably due less to declining overall stock than to changes in catchability or availability experienced by the expanding fishery in the localized area. The catch-effort relationship (Fig. 14) suggests little if any slowing of catches with increasing effective effort. Furthermore, a clear increasing trend in effective effort from 1969 to 1976 was lacking in either index or core areas (Table 2).

Catchability/availability changes are likely a function of evolving fishing tactics and of fish behavior. In particular, the rapid rise of CPUE in the small sport and starting-up joint-venture fisheries, after the cessation of longlining in Mexico's EEZ, was likely due to fish populations building up first and quickly in favored localities, which then become the natural focus of any renewed fishing. As these "hot spots" are again fished down, the fishery spreads out to include surrounding larger but lower catchability/availability areas. Overall CPUE thus at first decreases rapidly, then more slowly [such events are predictable from the tenets of optimal foraging theory (see Pyke et al 1977)]. The resulting CPUEs can therefore change rather strikingly with changes in the fishery, but not necessarily as a reflection of changes in overall stock size. Thus, adjacent coastal sport fisheries, located on the inner side of the aggregation area for striped marlin and whose fish are therefore first subjected to an external fishery, are affected (Fig. 15).

The eastern Pacific striped marlin is probably not overexploited. Nevertheless, its catch rates and fishery behavior warrant continual monitoring. This may be accomplished in relatively localized key or core areas where it may also be feasible to implement management measures such as closed seasons or areas, catch limits, etc. Such measures would best be implemented within the context of an international management regime. Lacking that, a coastal state may opt to act unilaterally if, by so doing, it can mitigate declines in the local catch rate. Core-area management off Mexico would recognize the importance of areas toward which fish aggregate and that, in such areas, differences in catchability/availability affect fishing tactics and CPUE trends. Quite possibly, and in general, changes in catchability/availability from the fishing down of localized "hot spots" may explain more of the proverbial "good old days" of fishing than the usual "fishing up" explanation (see Ricker 1975, p. 260).

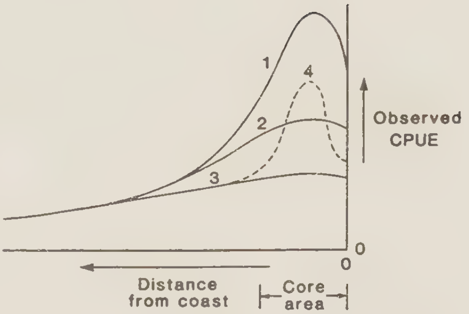

Figure 15. Hypothetical CPUE—distance profile showing effects of increased fishing (curves 1-3), followed by a rebuilding of the stock (curve 4). Catchability/availability is considered to decrease as the stock (CPUE) becomes less concentrated around the peak (peak broadens), which is where rebuilding occurs first.

A previous assessment by Bartoo and Ueyanagi (in Shomura 1980), using 1952-1975 data for north, south, and Pacific-wide "stocks," also concluded that there was no evidence for overexploitation. That study treated the entire data series as though it were applicable to a fully exploited stock although, in reality, the fishery had been expanding from west to east in the Pacific, at least up through the mid-1960s.

Literature Cited

Anonymous. 1962-1980. Annual reports of effort and catch statistics by area on Japanese tuna longline fishery. Fishery Agency of Japan.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest., Ser. II, Vol. 19. Her Majesty's Stationary Office, London.

Hanamoto, Eiji. 1974. Fishery-oceanographic studies of striped marlin, *Tetrapturus audax*, in waters off Baja California. I. Fishing conditions in relation to the thermocline. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972, Part 2, Rev. and Contr. Pap.:302-308.

Joseph, James, W. Klawe, and C. Orange. 1974. A review of the longline fishery for billfishes in the eastern Pacific Ocean. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp. Kailua-Kona, HI, 9-12 August 1972, Part 2, Rev. and Contr. Pap.:309-331.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. The Quart. Rev. Biol. 52(2):137-154.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Canada 191.

Shomura, Richard. 1980. Summary report of the billfish stock assessment workshop Pacific resource. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-5, 58 p.

Squire, James. 1987a. Pacific billfish angler catch rates for key area stock assessment. NOAA/NMFS, Mar. Fish. Rev. 49(2):15-25.

Squire, James. 1987b. Striped marlin *(Tetrapturus audax)* migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program: its relation to resource management. Mar. Fish. Rev. 49(2):26-43.

Squire, James and Z. Suzuki. 1989. Migration trends of striped marlin *(Tetrapturus audax)* resources in the Pacific Ocean. Current volume.

Wares, Paul and G. Sakagawa. 1974. Some morphometrics of billfishes from the eastern Pacific Ocean. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, August 9-12, 1972, Part 2, 107-120 p.

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Migration Trends of Striped Marlin *(Tetrapturus audax)* in the Pacific Ocean

James L. Squire and Ziro Suzuki

Migration patterns of large pelagic fish such as tunas and billfishes are not well defined in the Pacific Ocean, in spite of extensive tagging programs conducted for some of the species. Information on the potential for trans-oceanic or long-distance migrations has been developed for some species, but how population segments actually move is poorly known.

Investigators can determine migration trends by analyzing tagging data, length frequencies, and other biological differences by geographical areas, as well as the locations and seasonal movements of areas of high catch-per-unit-effort (CPUE). This paper reviews the biological and fishery charcteristics of striped marlin *(Tetrapturus audax)* to develop a hypothesis on their movements throughout the Pacific Ocean.

Development of the Fishery

In the post-World War II era, the Japanese longline fishing fleet expanded its operations until tunas and billfishes were fished in all tropical and temperate oceans of the world. By the early 1950s, the Japanese longline fleet had already explored the western, southwestern, and central Pacific areas for tunas and billfishes. (Honma and Kamimura 1958). By 1956, the Japanese longline fleet had reached into the eastern Pacific (E. of 130°W) (Suda and Schaefer 1965). Expansion continued through 1962, with fishing targeted on yellowfin tuna *(Thunnus albacares)* and bigeye tuna *(Thunnus obesus)* in the equatorial areas. At that time, tunas accounted for about 85% and billfishes for about 15% of the catch by weight. Billfish catches by number consisted of 9% blue marlin *(Makaira nigricans);* 4% striped marlin; and 1% of black marlin *(Makaira indica),* swordfish *(Xiphias gladius),* Pacific sailfish *(Istiophorus platypterus),* and shortbill spearfish *(Tetrapturus angustirostris)* combined.

A further expansion of the fishery occurred north of the equator in the early 1960s, with rapidly increased catches of striped marlin, sailfish, and swordfish. This increase occurred as the hooking rate of bigeye tuna declined in the eastern Pacific (Shiohama 1969). This final expansion completed the eastward exploration of the Pacific by the Japanese longline fleet.

Distribution of Striped Marlin

Fishing log records are maintained by longliners for the Japan Fishery Agency, and this organization has published catch and effort data annually on a worldwide basis for the years 1962 through 1980 (Anon 1962-1980). Biological data on striped marlin for many areas of the Pacific Ocean were also collected by Japanese fishery survey vessels and shore sampling, and these data have been published in various journals and reports.

Based on these Japanese data, various authors have attempted to describe the general distribution of striped marlin in the total Pacific or portions of it (Kume and Schaefer 1966, Kume and Joseph 1969, Howard and Ueyanagi 1965, Suda and Schaefer 1965, Nakamura 1974, Shiohama 1969, Honma and Kamimura 1958, Joseph et al 1974, Shingu et al 1974, Suzuki and Honma[1], Miyabe and Bayliff 1987). The general description of striped marlin distribution by Nakamura (1974), when modified to indicate low-catch-rate areas (Fig. 1), suggest that few striped marlin are found in the equatorial areas. Actually, data by Suzuki and Honma indicate low catch rates of <2.0 fish per 1,000 hooks in this area, possibly due to low catchability.

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[1] Suzuki, Ziro and M. Honma. 1977. Stock assessment of billfishes in the Pacific. Unpublished.

The relative size of the striped marlin population in various areas of the Pacific is of importance to this study. Results of the billfish stock assessment workshop (Shomura 1980) indicate that a considerable difference exists in population size between the north and south Pacific. For assessment purposes, the striped marlin population was divided at the equator. Areas of higher catch rates were observed in the northcentral, northeast, and southeast Pacific. The Pacific-wide stock was assessed as having a yield of 24,000 mt per year and the south Pacific estimate was 6,000 mt, about 1/3 that of the north Pacific yield. This significant difference in population size should be taken into account when comparing statistics for the various areas of the Pacific, particularly those for the southwest Pacific, an area of relatively low catch rate and population strength.

Movements of Striped Marlin

Evidence From Changes in CPUE

To determine how areas in the Pacific having high CPUE rates change, and to ascertain how these changes may relate to fish movements, the striped marlin CPUE data presented by Suzuki and Honma[1] were examined. For the period 1965-1975, the mean monthly CPUE values were ranked for each 5° long. by 5° lat. area. The 1965-75 period would cover years of full areal exploitation of striped marlin. Striped marlin occur as a by-catch in most areas of the

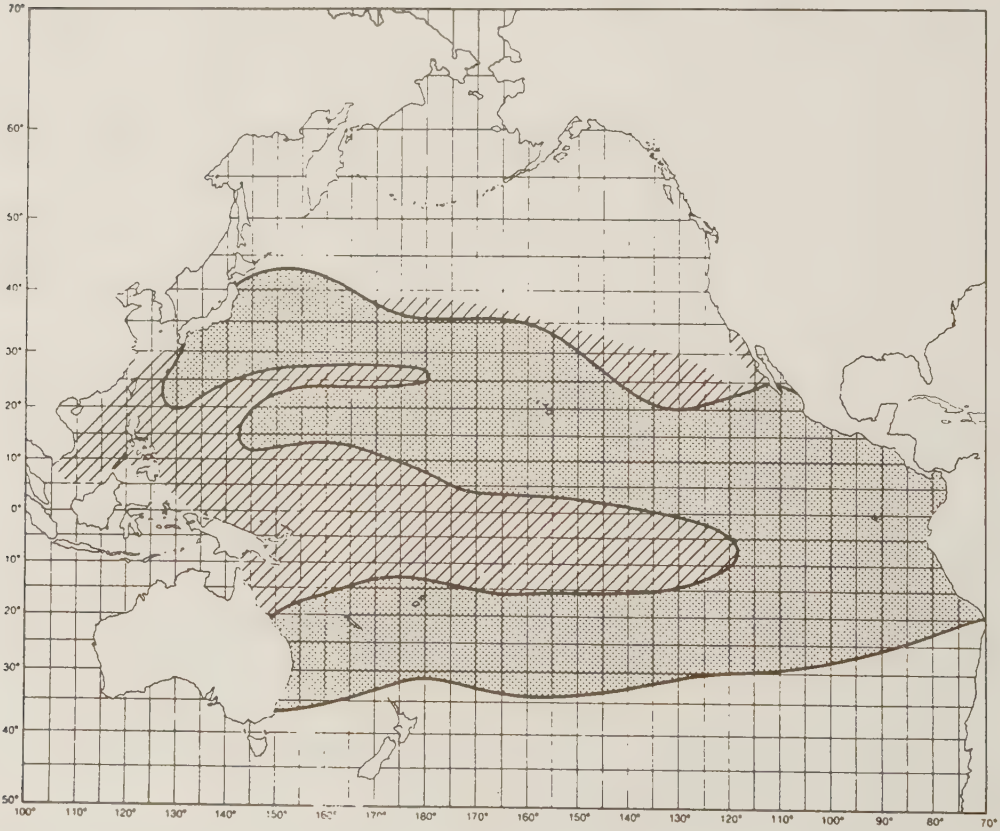

Figure 1. Distribution of good fishing grounds for striped marlin *(T. audax)* based on catch data from the Japanese longline fishery during 1964-1969 (adapted from Nakamura 1974). Light stippled areas indicate striped marlin occurrence, but at low catch levels.

Pacific except the eastern Pacific, where the species is targeted. Changes in catchability that result from targeting or non-targeting the species should not mask main patterns. Areas having an average CPUE value of 2.1 to 5.0 striped marlin per 1,000 hooks fished were assigned a value of 1, and areas having an average CPUE value of 5.1 striped marlin or more were assigned a value of 2. The monthly ranks were summed for all 12 months in each 5° longitude by latitude area where striped marlin catch exceeded 2.1 fish per 1,000 hooks (Fig. 2). The highest CPUE value (24) is found near the southern tip of Baja California, Mexico. The highest value (24) means that an average CPUE level of 5.1 striped marlin or greater occurred for all months during 1965-1975. Smaller numbers represent lesser sums of the ranking of mean monthly CPUE values. The areas to the south and southeast, off Ecuador and near the Galapagos Islands, have high CPUE values, as do areas further southwest, from 10° to 30°S lat. along 100°W long.

The highest CPUE values in the northeast Pacific were observed from June to November, while highest values in the southeast Pacific were apparent from December to March. In the southwest Pacific, CPUE values were highest in the Coral Sea area from October through January. In the north and north-central Pacific, highest CPUE values were observed north and west of the Hawaiian Islands from April to July.

Based in part on information on the movements of striped marlin from Honma and Kamimura (1958) for the southwest Pacific, Shiohama (1969) for the eastern Pacific, and Suzuki and Honma[1] for the total Pacific, we now infer seasonal movements of striped marlin from areal changes of high CPUE (Figs. 3 to 6, wherein arrow length indicates the approximate

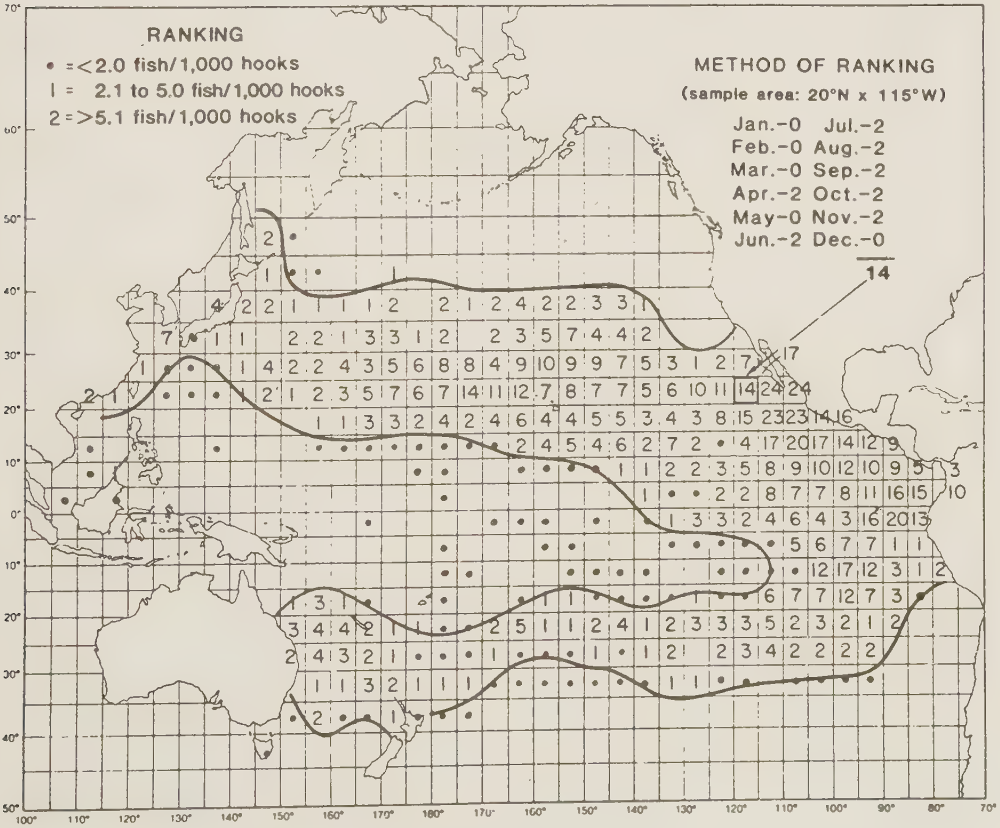
RANKING
• =<2.0 fish/1,000 hooks
1 = 2.1 to 5.0 fish/1,000 hooks
2 =>5.1 fish/1,000 hooks
METHOD OF RANKING
(sample area: 20°N x 115°W)
Jan.-0 Jul.-2
Feb.-0 Aug.-2
Mar.-0 Sep.-2
Apr.-2 Oct.-2
May-0 Nov.-2
Jun.-2 Dec.-0
14
70°
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
100°
110°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°

Figure 2. Rank values for hooking rates (CPUE) by Japanese longliners. Numbers represent the sum of mean monthly rank values for CPUE, 1965-1975.

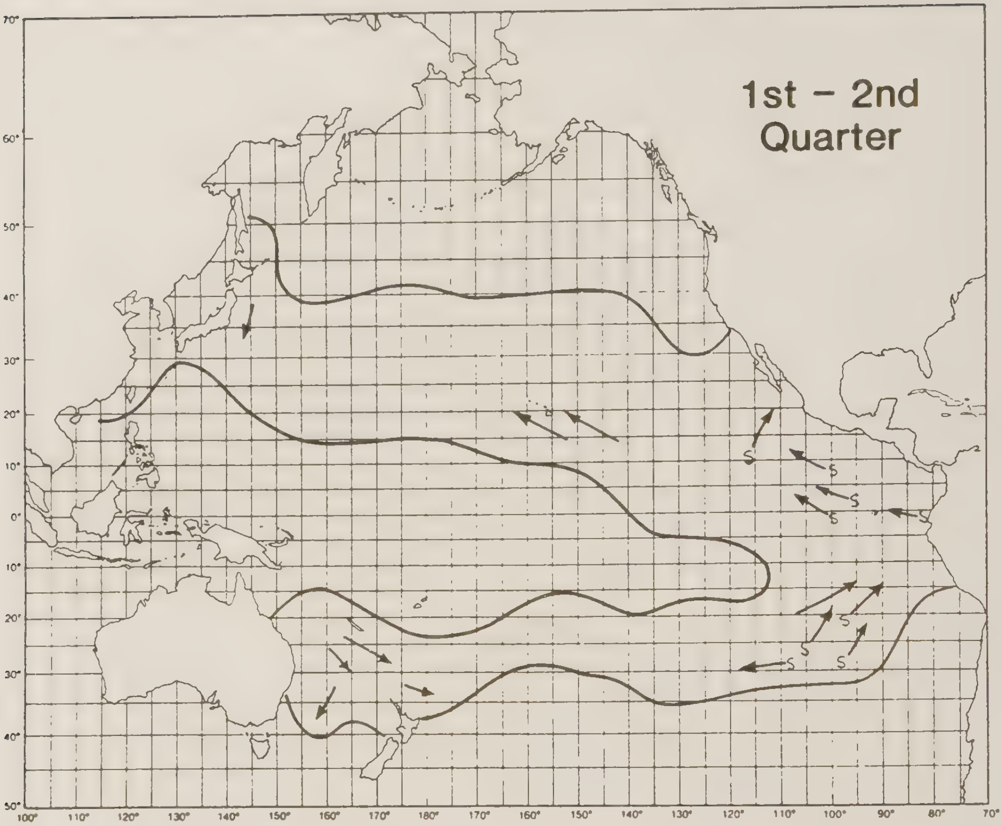

Figure 3. Trend of striped marlin CPUE movement from the first to second quarter. "S" indicates observations of Shiohama (1969).

geographical movement of higher CPUE areas).

In the southwest Pacific, striped marlin CPUE levels are low compared to those observed for the eastern and north Pacific, though seasonal changes are still evident. Fishing grounds north of New Zealand orient east to west at 16°-30°S latitude. The major fishing season is from August to January, with catches peaking in October and November. There is a west-northwest migration of high-CPUE areas to about 22°S lat. from August to November (Fig. 5) and migration is to the south to southeast after November (Fig. 6) and into the southern summer (Fig. 3). Honma and Kamimura (1958) reported a modal size group of 200 cm (eye-fork length) which was observed to be constant throughout the fishing season.

In the south-central Pacific high-CPUE areal movement to higher latitudes during the second and third quarters (Fig. 4) can be detected. There is some evidence of eastward movement from the third to fourth quarters (Fig. 5) and additional evidence of movement to the southeast Pacific area from the fourth to first quarters (Fig. 6).

In the northwest Pacific (W. of 165°E), there is evidence of a west to northwest movement of high-CPUE during the second to third quarters (Fig. 4) and evidence of a south to southeast migration during the third to fourth quarter (Fig. 5).

In the north-central Pacific (165°E to 130°W), high-CPUE movement to the east and northeast is noted from the second to third quarters (Fig. 4), shifting to a southwesterly movement in the early fall (September, Fig. 5). This movement continues through the fall and winter (Fig. 6) then shifts to a northwestward movement during the spring (March; Fig. 3).

In the eastern Pacific (E. of 130°), three areas have high CPUE levels (Fig. 2). Their areal

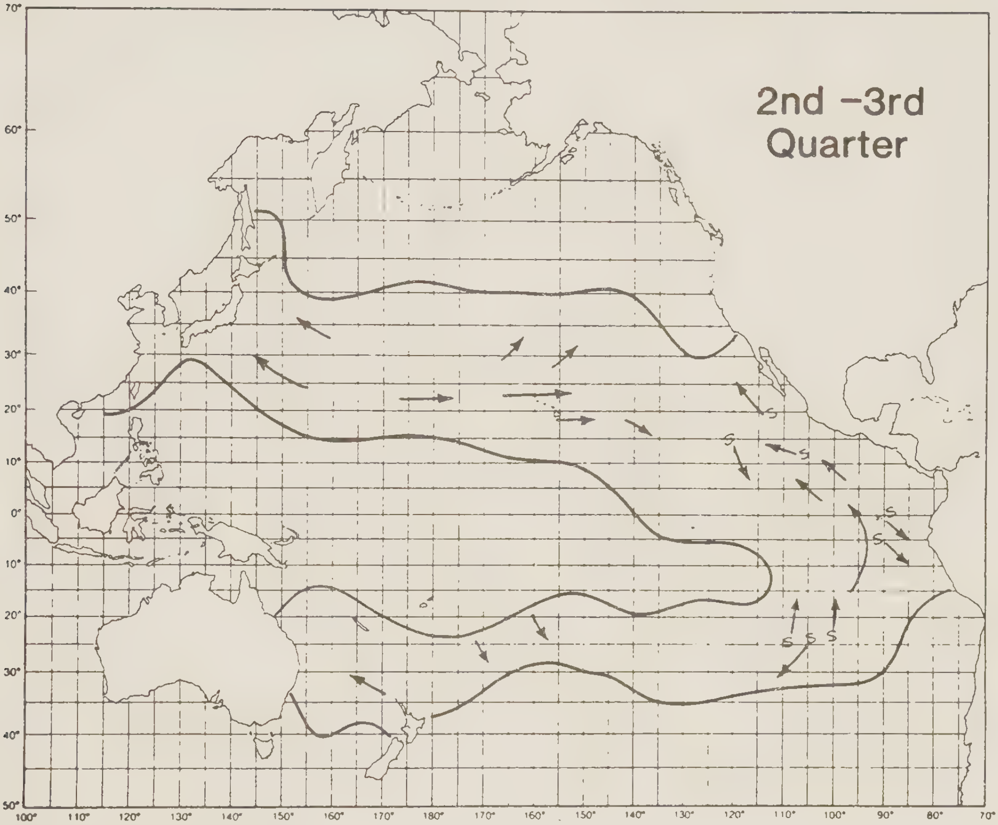

Figure 4. Trend of striped marlin CPUE movement from the second to third quarter.

changes during the first to second quarter (Fig. 3), shows a northwest movement toward Baja California from off Central America, a north to northeast movement towards the Galapagos Islands and Ecuador area, and a weaker movement toward the west at 110°W long, and 25° to 30°S lat. The change in CPUEs in the second to third quarters (Fig. 4) appears to be similar; areas of high CPUEs shift northwestward along the west coast of Mexico toward the high-CPUE areas off Baja California. A definite shift of high-CPUE areas occurs from the southeast to the northeast Pacific and there is a shift southeast of higher CPUE rates off Ecuador from the Galapagos Island area. Between the 3rd and 4th quarter, there is a shift in high-CPUE areas to the southwest off Baja California and a southeast shift toward the southern hemisphere in the offshore area off Mexico and Central America (90°-100°W long. by 5°-15°N lat.) (Fig. 5). The migration pattern southwest of the Galapagos Islands appears to be reflected in the shift toward the high-CPUE areas observed during the winter and spring months, centered about 10°-15°S lat. by 95°-100°W long.

The fourth to first quarter of the year in the northeast Pacific (Fig. 6) shows a reverse of the observations made during first to second and second to third quarter. The areas of high CPUEs shift to the southeast from the Baja California area and offshore central Mexico. A shift to the east with separate movements from the northwest and the southwest is evident in the southeast Pacific. This movement is again toward an area of high CPUE levels observed southwest of the Galapagos Islands (Fig. 2).

The foregoing longline CPUE data, from logbook summaries of catch and effort produced by the Japan Fishery Agency, must be used with caution. These data lack details needed for accurate interpretation of CPUE. Longline gear may be fished in many ways to target on specific species. Target species are not indicated on the fishing log. From sampling reported by Suzuki and Honma[1], longline gear appears to capture mostly large, older fish. Only a small percentage of striped marlin is reported at 90 cm (eye-fork) or less. The minimum and maximum sizes reported were 30 cm and 290 cm, respectively. Longline gear has the capability of capturing striped marlin over a considerable range of sizes (and ages), but data from this gear may be more applicable to the older fish. Finally, areal changes in CPUE could reflect changes in catchability or availability rather than movement.

Longline summary data (Suzuki and Honma[1]) can, nevertheless, give consistent results, and have previously been used in an analysis of tagging results for black marlin tagged in the Coral Sea off the Great Barrier Reef, Queensland, Australia (Squire and Nielsen 1983). Initial movement of tagged black marlin was generally in a southeast direction, parallelling the change of the longline CPUE rate. In the northeast Pacific, the seasonal change of high longline CPUE values for striped marlin also paralleled the movement of tagged striped marlin (Squire 1987).

Evidence From Tagging

Tagging programs for billfishes have resulted in over 12,000 striped marlin being tagged and released, with most of the fish tagged and released by anglers in the northeast Pacific off Baja California. Information from the tagging program is generally limited to migration rates and direction and distance of striped marlin routes in the northeast Pacific (Squire 1987).

The percentage of striped marlin recovered is low (about 1%). This low return rate is a common feature of billfish tagging programs in both the Pacific and Atlantic (Mather et al 1974, Squire and Nielsen 1983, Squire 1987). This may be due to tag loss, either from increased

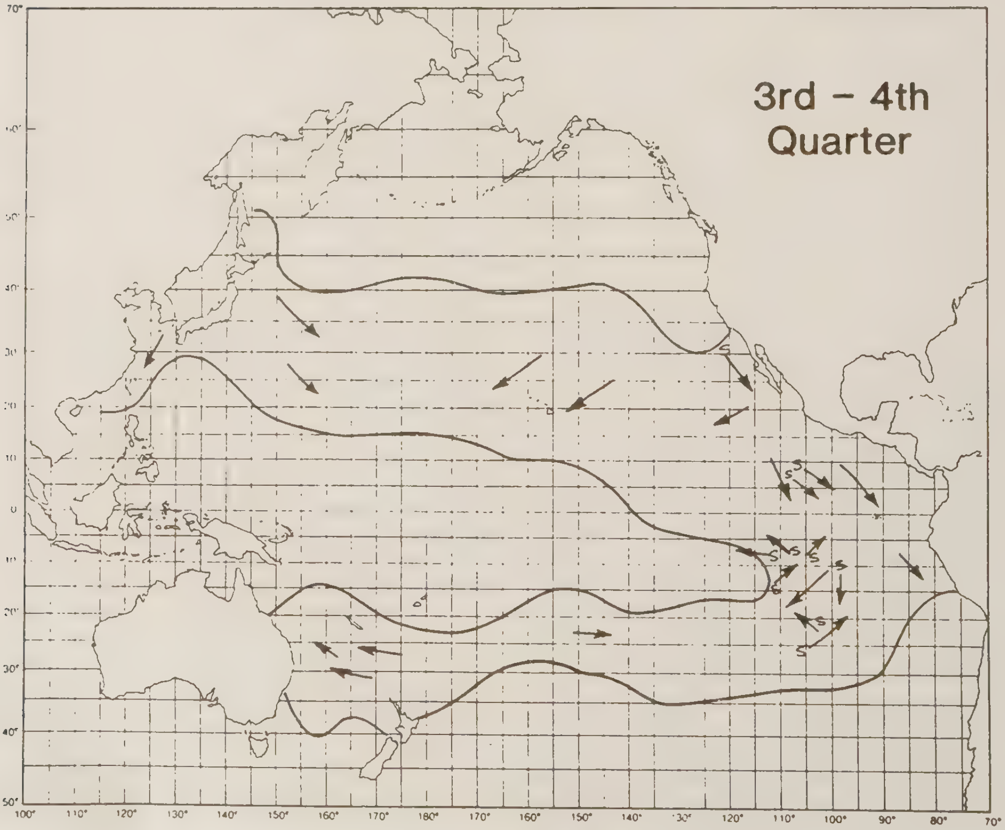

Figure 5. Trend of striped marlin CPUE movement third to fourth quarter.

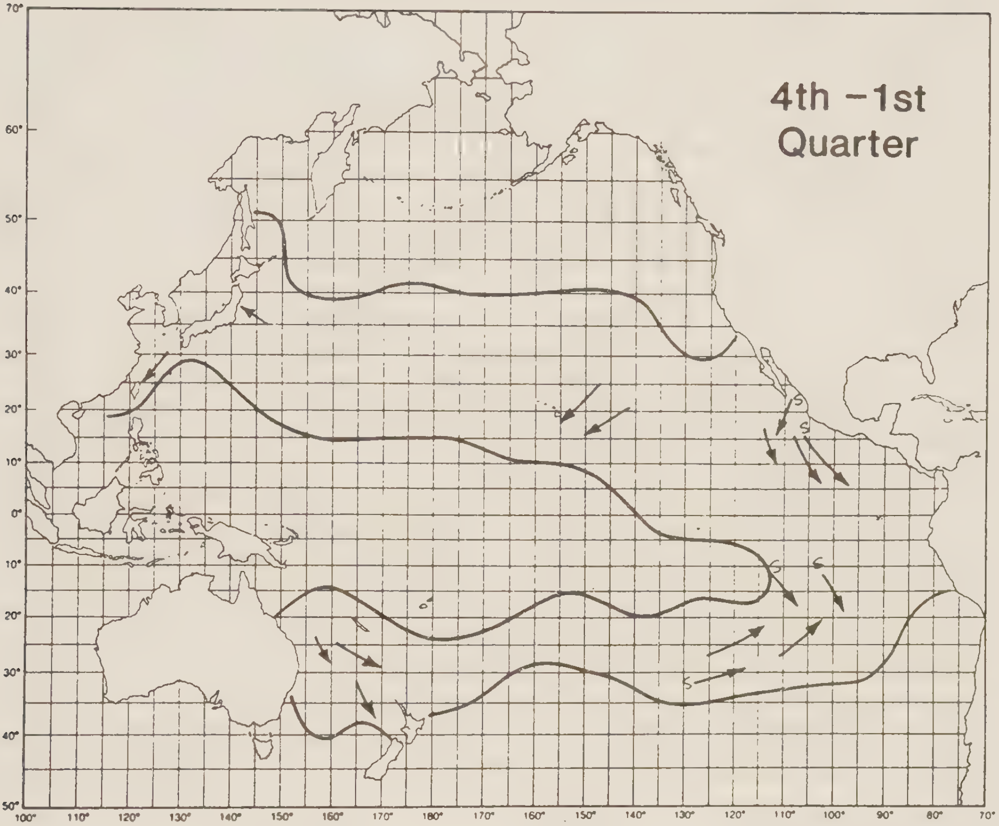

Figure 6. Trend of striped marlin CPUE movement fourth to first quarter.

mortality due to hooking, or from tag shedding, or to a combination of factors. Another unknown in evaluating the frequency of long-term recoveries is behavioral changes in migration patterns related to age. As striped marlin become older, they may move away from the highly productive "target fishing areas" into less frequently fished areas. This would tend to reduce the chance of recapture. In the northeast Pacific, length-frequency data (1965-1976 and 1980-1983) from the longline fishery (Suzuki and Honma[1]; M. Comparan, pers. comm.) would indicate that the larger size fish (older year classes) are not represented in the catch as they are in other areas of the Pacific. These factors may limit the ability of billfish tagging results to describe accurately the interactions between populations observed in various geographical areas of the Pacific.

A hypothesis describing the seasonal trend of striped marlin migration in the northeast Pacific was given by Squire (1987). Using plots of tag and recovery points, migration direction and rate analyses, movements of high-CPUE areas in the commercial longline fishery over time, and the spawning behavior exhibited in the northeast Pacific, he developed a schematic of seasonal migration. The movements can be shown in the form of time periods and distance of recovery points from the tagging site (Fig. 7) for time periods 0-60, 61-120, 121-240, and 241-360 days after tagging and release to recapture. Some of the tagged fish return to the tagging area; however, most returns were short-term (<1 year).

Long-range and non-seasonal movements from one area of the Pacific to another has been shown for some striped marlin tagged off Baja California, but a greater percentage of distant-water recoveries to the west and southwest has resulted from the limited tagging off southern California. Most recoveries from southern

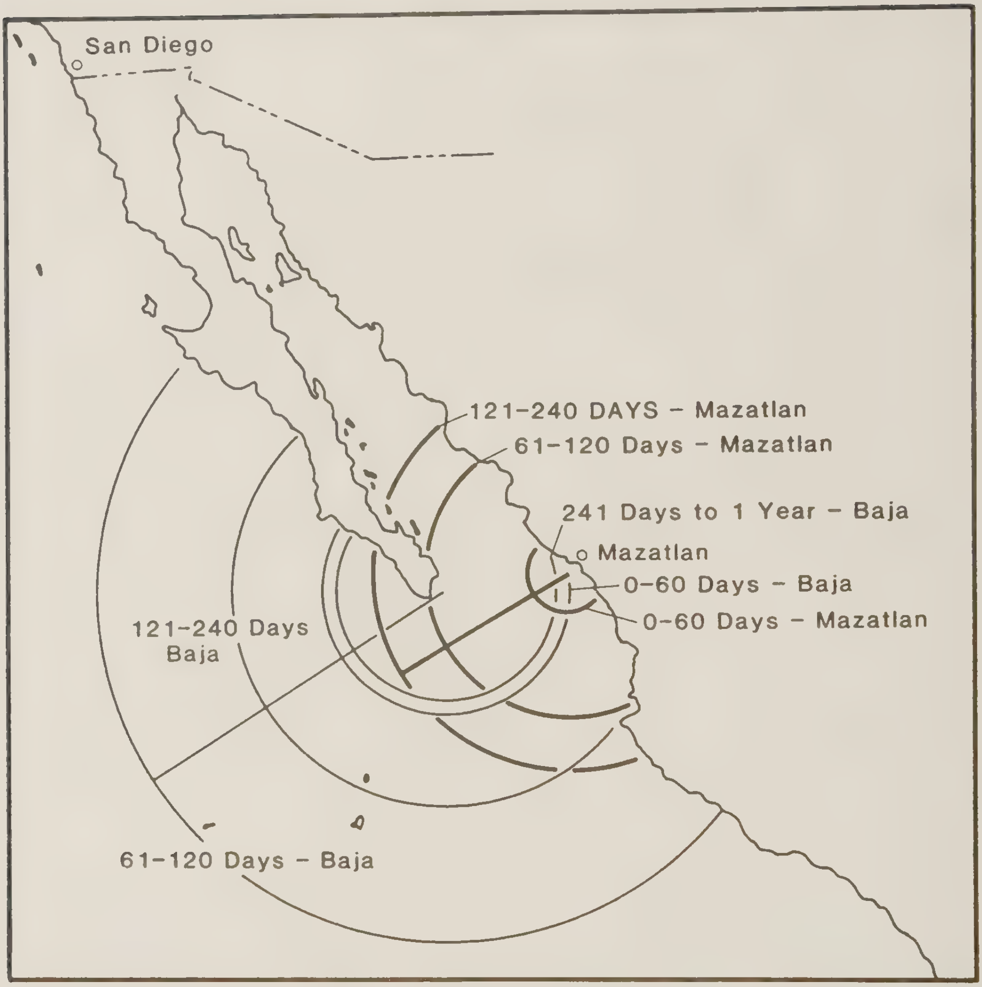

Figure 7. Average midpoint migration distances from tagging areas off Baja California Sur and Mazatlán to recapture points for time periods, tagging to recapture, 0-60, 61-120, 121-240, and 241 days to 1 year.

California tagging have been made to the southeast off Baja California, the most distant at 113°W long. by 20°S lat. Several recoveries have been made near the Hawaiian Islands, indicating that some movement is to both the north-central and southeastern Pacific from off southern California.

In January 1983, a striped marlin was reported tagged off Cabo San Lucas, Mexico, and was recovered near Norfolk Island, north of New Zealand, in September 1984. This fish was identified by the angler and charter boat captain at the time of tagging as a striped marlin; upon recapture, it was reported by the vessel's agent in New Zealand as a black marlin. The body and dorsal fin differences between a striped marlin and a blue marlin or black marlin are sufficient for identification at the time of tagging; therefore, this recovery was assumed to have been a striped marlin.

Further to examine the relationship of striped marlin tagged in the northeast Pacific to the remainder of the eastern Pacific population, the CPUE trend was compared over time between the major "target areas" for commercial and recreational fishing (and tagging) of striped marlin off Baja California (20°N lat. by 105° and 110°W long.) and the longline CPUE trend observed for the total eastern Pacific (east of 130°W long.). There is a good association between fluctuations in CPUE for the target area off Baja California (which accounts for about 23% of the striped marlin caught by the longline fleet in the eastern Pacific) and fluctuations in CPUE for the total eastern Pacific (Fig. 8). This indicates mixing between populations in the eastern Pacific at rates greater than suggested by tagging results for the Baja California area (Squire 1987). In studies of the Japanese longline fishery around Baja California, Squire and Au (1990) observed a rapid rebuilding of the striped marlin population following cessation of longline operations within Mexico's EEZ. This population increase was attributed to immigration from other areas of the Pacific into the major feeding and growth area in the northeast Pacific.

Evidence From Spawning Areas

Although spawning has been identified in the eastern Pacific by studies of gonad indices (Joseph et al 1974, Squire 1987), biological surveys to date have failed to identify this area as a major spawning location in the Pacific. The surveys include those by EASTROPAC, IATTC, and the billfish spawning surveys conducted south of Baja California, Mexico, in 1968 by the U.S. Fish and Wildlife Service.

Spawning in the western Pacific on the other hand has been well established through extensive collection of striped marlin larvae in the central and western Pacific (Ueyanagi 1959, 1974; Nishikawa et al 1985). Honma and Kamimura (1958) reviewed the southwest Pacific fishery for striped marlin and it was evident that the seasonal movement of the fishery is in positive relationship to the spawning season and area. In the eastern Pacific, tagging has indicated that striped marlin likewise tend to migrate rapidly southward of the southern tip of Baja California in the summer into an area of reported but unverified spawning (Squire 1987).

During the summer, larval and juvenile fish in the proposed spawning areas of the northeast Pacific should be carried to the west in the North Equatorial Current. Little is known of spawning in the southeast Pacific, although concentrations of striped marlin are evident there during the southern summer (5°-10°S × 100°-110°W). If this concentration is a spawning population, then the larvae and juveniles would drift westward in the South Equatorial Current.

Ueyanagi's (1974) and Nishikawa's (1985) larval distribution charts indicate that many larvae occur in the north-central to northwestern Pacific between the equator and 30°N latitude, and in the south Pacific between 10°S and 25°S

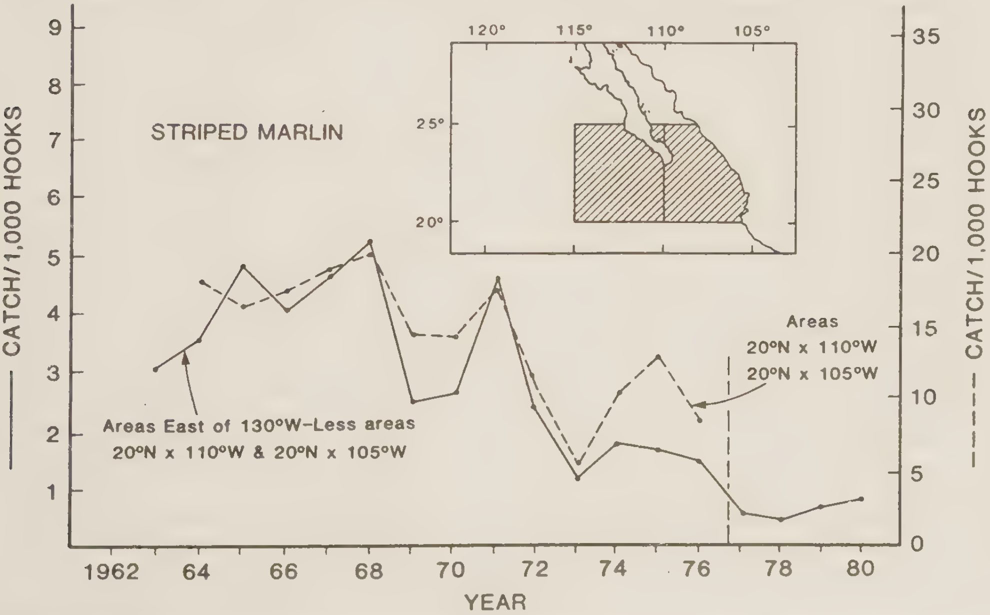

Figure 8. Comparison of CPUE trends for areas around Baja California (20°N × 105° and 110°W) and for the total eastern Pacific, less these areas.

latitude. No collections of larvae are reported east of 135°W longitude. During the summer, the current and larval drift there is westward in the North Equatorial Current, although some larvae and juveniles may drift to the east in the lower latitudes in the North Equatorial Countercurrent. In the southern hemisphere, spawning during the southern summer should result in larval and juvenile drift to the northwest.

Data from the fishery indicate that younger fish (<110 cm eye-fork) are concentrated in the north-central Pacific area, with lesser concentrations in the northwest and south central Pacific. These data, plus the dearth of larvae in the eastern Pacific — even when considering westward transport of larvae by the currents — suggest that mature fish are less likely to reside in the eastern Pacific.

Evidence From Biometrics

In 1956, Kamimura and Honma (1958) made a biometric comparison of the external characteristics of striped marlin from the north Pacific (30°-35°N) and the south Pacific (18°-25°S). Among five morphometric characters measured, a noticeable difference was observed only in pectoral fin length relative to the eye-fork length. Biological sampling (morphometrics) of striped marlin in the eastern Pacific, about the southern tip of Baja California and Mazatlan, Mexico, and southern California in the late 1960s, was reported by Wares and Sakagawa (1974). They found no differences between samples taken from off southern California and those off Mexico in the relationship of pectoral fin length and eye-fork length. Data from Wares and Sakagawa (1974) and Royce (1957) were replotted on the graphic from Kamimura and Honma (1958) for pectoral length vs. body (eye-fork) length (Fig. 9). In Honma and Kamimura's (1958) study, the difference between pectoral fin-body length relationships in the northwest and southwest Pacific appears to be size related. In the northeast Pacific, pectoral fin length (compared to eye-fork length) overlapped that of both the northwest and southwest Pacific.

Fin length and other minor differences in morphology are not supported as species-differentiating characters in other studies of pelagic species such as yellowfin tuna (Schaefer et al 1963, Mimura 1963). Royce (1957) examined fish from the central and eastern equatorial Pacific (Fig. 9). Wares and Sakagawa (1974), in reporting the findings of Kamimura and Honma (1958) and Royce (1957), concluded that there appears to be "mixing in the central Pacific of the presumed south and north stocks, of striped marlin, or Kamimura and Honma's samples did not adequately reflect the degree of variability in length of pectoral fin of fish from the north and south Pacific." It is possible that striped marlin exhibit allometric growth, and that the larger sizes have longer pectorals relative to eye-fork length. Data on pectoral fin lengths presented to date would indicate the possibility of a cline in the Pacific between the northwest and southwestern Pacific, with broad overlap into the eastern Pacific.

The concept of a stock cline seems appropriate for two reasons: the distributon of striped marlin in the Pacific is of a continuous "horseshoe shape" (north Pacific, eastern Pacific, and south Pacific); and the population in the northeast Pacific has characteristics that are representative of both the northwest and southwest Pacific (Wares and Sakagawa 1974). It appears unlikely, for reasons of proximity alone, that the southwestern population is distinct or separated from the remainder of the Pacific. However, it is possible that the population in the southwest Pacific is associated with the populations in the Indian Ocean, even though striped marlin are not caught in any substantial quantity from the Coral Sea to the Indian Ocean, and the size frequency is different from the two areas (Suzuki, pers. comm.). The southwest Pacific appears, instead, to be an area preferred by large, but not smaller, striped marlin.

Evidence From Changes In Modal Length

Examination of Japanese commercial longline length-frequency data (eye-fork lengths in cm) taken for six areas of the Pacific (Suzuki and Honma[1]) reveals a progression of modal changes among the six areas. Data for modal lengths (and the maturity point of about 160 cm; Ueyanagi and Wares 1975), spawning areas, and higher catch-rate areas (Fig. 10) can be used to infer trans-Pacific (long-range) movements of (Pacific) striped marlin over an extended time period (several years).

The north-central Pacific (Area I — east of 130°W long. and north of the equator to 20°N lat.) has within its boundaries the major areas of spawning as indicated by larval fish abundance. The catch sample for the north-central area represents 212,600 striped marlin. Only this area shows a bimodal frequency distribution with

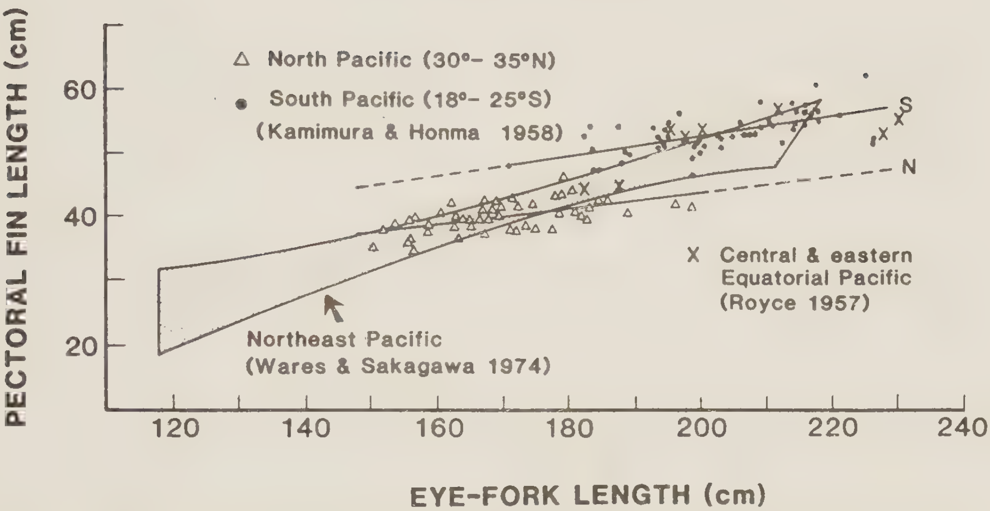

Figure 9. Relations between striped marlin pectoral fin length and body length in the north and south Pacific (Kamimura and Honma 1958), in the northeast Pacific (Wares and Sakagawa 1974), and in the central and eastern Equatorial Pacific (Royce 1957).

young fish (mode 110 cm) nearly equaling the abundance of older fish (mode 160 cm). The first mode at 110 cm (=10-18 kg fish) was composed of fish ranging in size from 80 to 130 cm, representing immature fish seldom observed in the other areas, except Area II and Area Ia to a lesser degree. Approximately 25% of the fish sampled were within the range of 80 to 130 cm, and an estimated 55% of the sample was of immature sizes (<160 cm). The second mode was at 160 cm, with the maximum size recorded at 270 cm.

The northwest Pacific (Area II — north of 20°N lat. and east of 130°W long.) sample represents a catch of 757,400 fish; the modal length is 160 cm, which also represents about a 50% point, immature to mature fish. The numbers of fish of the smaller modal size of 80 to 130 cm observed in Area I were greatly reduced. A small mode of 230 cm fish is recorded.

The south-central Pacific (Area Ia — 0° to 10°S lat. and west of 130°W long.) is an area of lower catch, with the sample representing a total catch of 22,900 fish. The modal length in this area is 10 cm larger than in Area I, with an estimated 60% of the fish catch being above the maturity point of 160 cm. The 80 to 130 cm group, the range so substantially represented in Area I is observed, but even less so than in Area II.

For the northeast Pacific (Area III — north of 10°N lat. and east of 130°W long.), the sample represents a catch of 611,900 fish and the modal size was 170 cm, 10 cm larger than that observed for the northwest Pacific (Area II). About 65% of the fish catch is within the mature range $\geq$160 cm), but fish under 95 cm and fish over 210 cm were not observed, making this area the most constricted in length-frequency range. Only a small portion of the sample was of the 80 to 130 cm size group observed in the north-central or northwest Pacific (Areas I and II).

The southeast Pacific (Area IV — east of 130°W long. and south of 10°N) sample represents a catch of 498,000 fish and the modal length was 180 cm, 10 cm larger than that observed for the northeast Pacific. The size frequency range was greater than observed in the northeast Pacific (80 to 265 cm). The 80 to 130 cm group observed in the west-central Pacific represents only a small percentage of the catch. About 75% of the catch is estimated to be in the mature range. As observed for the northeast Pacific, few adults larger than 210 cm were sampled. In contrast to these eastern Pacific areas, the other areas had evidence of larger fish with small modes at 210 cm (Area I), 230 cm (Area II) and 260 cm (Areas Ia and V).

The southwest Pacific (Area V — east of 130°W long. and south of 10°S) sample represented a catch of 498,400 fish and showed an increase in modal size to 190 cm, again a 10 cm increase over the southeast Pacific and a 20 cm increase over the south-central Pacific. Only

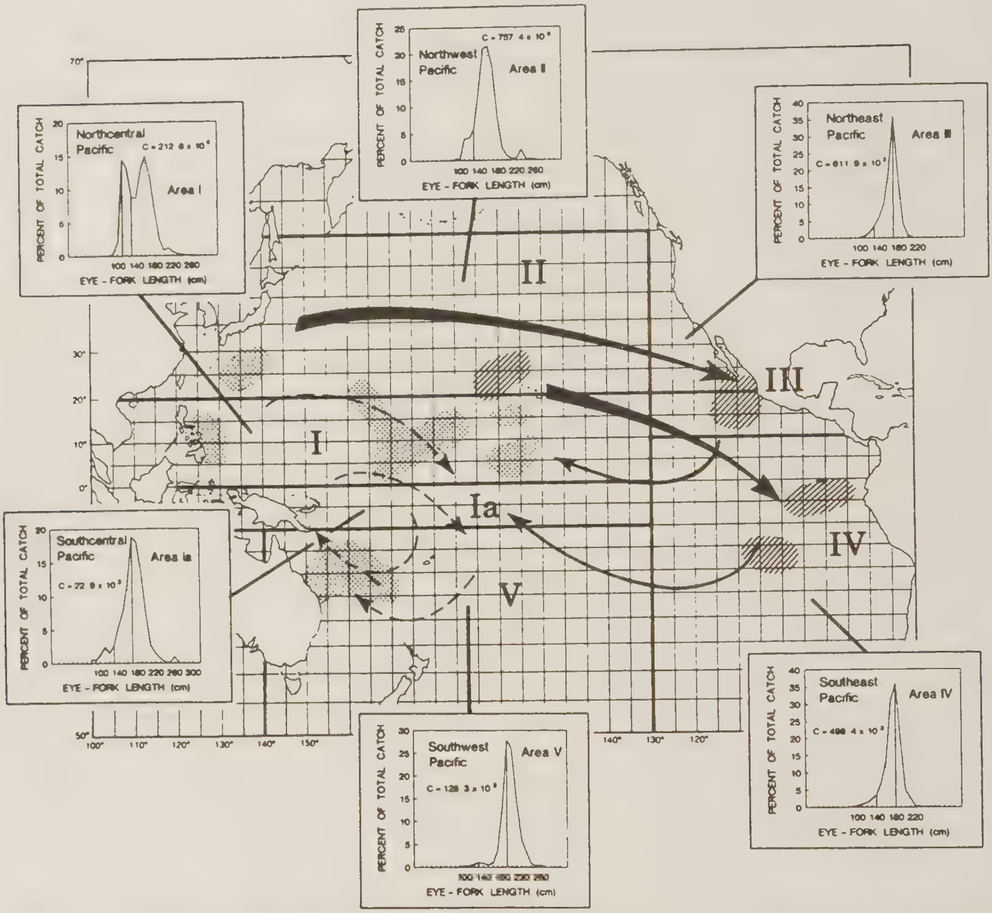
Northcentral Pacific
C = 212 8 x 10³
Area I
PERCENT OF TOTAL CATCH
0 5 10 15 20
100 140 180 220 260
EYE - FORK LENGTH (cm)
Northwest Pacific
C = 757 4 x 10³
Area II
PERCENT OF TOTAL CATCH
0 5 10 15 20 25
100 140 180 220 260
EYE - FORK LENGTH (cm)
Northeast Pacific
Area III
C = 611 9 x 10³
PERCENT OF TOTAL CATCH
0 5 10 15 20 25 30 35 40
100 140 180 220
EYE - FORK LENGTH (cm)
Southcentral Pacific
Area Ia
C = 72 9 x 10³
PERCENT OF TOTAL CATCH
0 5 10 15 20
100 140 180 220 260 300
EYE - FORK LENGTH (cm)
Southwest Pacific
Area V
C = 128 3 x 10³
PERCENT OF TOTAL CATCH
0 5 10 15 20 25 30
100 140 180 220 260
EYE - FORK LENGTH (cm)
Southeast Pacific
Area IV
C = 498 4 x 10³
PERCENT OF TOTAL CATCH
0 5 10 15 20 25 30 35 40
100 140 180 220
EYE - FORK LENGTH (cm)
I
Ia
II
III
IV
V
70°
30°
20°
10°
0°
50°
100° 110° 120° 130° 140° 150°
140° 130° 120°

Figure 10. Distribution of length frequencies (eye-fork lengths) observed 1967-1973 in 6 areas of the Pacific Ocean, and a general scheme of movement. Heavy arrows indicate, for younger fish, the eastward clockwise movements for feeding and growth and the westward return to the spawning areas. Dashed arrows indicate similar movements of large, older fish. Movements of intermediate-aged fish would be intermediate between the patterns shown.

a small percentage of fish were observed in the 80 to 130 cm size and an estimated 85% of the fish were above the maturity breakpoint of 160 cm.

The increase in modal lengths from the north-central to northwestern and south-central, and from the northwestern to northeastern and south-eastern and to the southwest Pacific, would appear to be a reflection of the effects of long term defusive migration between the various geographical areas (Fig. 10.

Summary

From examination of the geographical locations of the major known spawning areas, the distribution of length-frequency modes, differences in morphometrics, and changes of high-CPUE areàs in the commercial longline fishery, a generalized migration pattern can be hypothesized:

- The major spawning area is in the western Pacific (north-central to western). Some spawning may occur in the eastern Pacific but few larvae have been caught there. There is also spawning in the southwest Pacific. Only a small percentage of young fish is caught in the northeast, southeast, and south-west Pacific, whereas a large percentage of small fish are observed in the catch in the north-central Pacific; the percentage declines in the northwest and south-central Pacific. Small fish are more common westward from the central Pacific. Young fish (larvae or juveniles) may migrate or drift westward from the major spawning area in the North Equatorial Current and, as they grow, some may move into the northwest and south-central Pacific. Sizable numbers of juvenile striped marlin must, however, migrate to the northeast and southeast Pacific areas, which are the most productive for fish of 170 and 180 cm (eye-fork length).

- Changes in areas with high CPUE values indicate local migrations that parallel the seasonal changes of the total environment (physical and biological); i.e., poleward during the northern and southern summers in the respective hemispheres. Changes in migration patterns with growth in size is likely.
- Modal shifts in eye-fork length can be observed from length-frequency data (Fig. 10), which indicate a shifting of individuals over time from the north-central to the northwest and south-central Pacific, and to the north and southeast Pacific, and then to the southwest Pacific. Modal data indicate that the north-central, northwestern, and south-central areas have populations of both old and young fish, while the northeastern and southeastern areas have intermediate-sized individuals.

In their publication on tunas and billfishes, Joseph et al (1979) describe tunas as "wandering fish," and this description could also be applied to striped marlin. From tagging evidence, however, striped marlin cannot be described as "highly migratory" in the sense that rapid trans-ocean migrations are as common as for such species as bluefin tuna *(Thunnus thynnus)* and albacore tuna *(Thunnus alalunga)*.

Evidence suggests that a net long-term movement occurs from areas having high percentages of smaller fish to areas with larger fish. The indicated long-term movement between the north-central Pacific, an area with small fish, to the southeast and northeast Pacific, and the movement of fish back to the west as they grow, appears to be slow. The larger sizes (>200 cm) are not present in the northeast and southeast Pacific, indicating that these areas are more important as feeding than as spawning areas for intermediate size fish. After a period of time in the eastern Pacific, the maturing fish probably wander back westward to the major spawning areas, and the larger sizes thereafter tend to remain closer to the spawning areas in the western Pacific. A possibility exists of an identifiable population in the southwest Pacific, based on pectoral fin length; however, data from other areas tend to refute this possibility even though indicating a gradation or cline of pectoral fin lengths — which may be due to allometric growth.

The migration patterns of striped marlin appear as a general movement that would indicate a stock relationship among all areas in the Pacific. This relationship may be similar to that of yellowfin tuna in the Pacific (Suzuki et al 1978) as "semi-independent subpopulations" in the high-abundance areas. The actual interchanges among areas will be difficult to determine because, throughout the Pacific, these fish seasonally move poleward and back and between feeding and spawning areas, their availability alternately increasing and decreasing in the geographical areas that are centers for feeding or spawning. Depending upon maturity and feeding conditions, some fish will range farther than others, and it is possible that most may move, in time, to most other areas of the Pacific. Overall movements, however, are diffusive over years rather than highly migratory, and this circumstance should permit management by "stocks."

Acknowledgement

The authors wish to recognize the assistance of Dr. David Au in the preparation of this paper. His perception of behavior characteristics of pelagic species has been of great help in preparation of this hypothesis of striped marlin migration.

Literature Cited

Anonymous. 1962-1980. Annual report of effort and catch statistics by area on Japanese tuna longline fishery. Research Department, Fisheries Agency of Japan.

Honma, M. and T. Kamimura. 1958. A population study on the so-called Makajiki (striped marlin) of both northern and southern hemispheres of the Pacific. Rep. Nankai Reg. Fish. Res. Lab. 1958(3):12-21.

Howard, J. and S. Ueyanagi. 1965. Distibution and relative abundance of billfishes (Istiophoridae) of the Pacific Ocean. Stud. Trop. Oceanogr. (Miami) 2, 134 p.

Joseph, J., W. Klawe and C. Orange. 1974. A review of the longline fishery for billfishes in the eastern Pacific Ocean. NOAA Tech. Rep. SSRF-675(2):309-331.

Joseph, J., W. Klawe and P. Murphy. 1979. Fish without a country. 1st edition, Dec. 1979, Inter. Am. Trop. Tuna Comm., La Jolla, CA.

Kamimura T. and M. Honma. 1958. A population study of the so-called Makajiki (striped marlin) of both northern and southern hemispheres of the Pacific. I. Comparison of external characters. [In Jap., Engl. summ.] Rep. Nankai Fish. Res. Lab. 8:1-11.

Kume, S. and M. Schaefer. 1966. Studies on the Japanese longline fishery for tuna and marlin in the eastern tropical Pacific Ocean during 1963. Inter-Am. Trop. Tuna Comm. Bull. 11(3):103-170.

Kume, S. and J. Joseph. 1969. The Japanese longline fishery for tunas and billfish in the eastern Pacific Ocean east of 130°W, 1964-1966. Inter. Am. Trop. Tuna Comm. Bull. 13(2):275-418.

Mather, F., J. Mason, and L. Clark. 1974. Migrations of white marlin and blue marlin in the western Atlantic Ocean — Tagging results since 1970. In Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972. NOAA Tech. Rep. SSRF-675(2):211-225.

Mimura, K. 1963. Synopsis of biological data on yellowfin tuna *Neothunnus macropterus*, Temminck and Schlegel, 1842 (Indian Ocean). *In:* Proc. Int. World Sci. Meeting on the Biology of Tunas and Related Species. FAO Fish Rep. 6(2):319-349.

Miyabe, N. and W. Bayliff. 1987. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean 1971-1980. Inter-Am. Trop. Tuna Comm. Bull. 19(1):1-163.

Nakamura, I. 1974. Some aspects of the systematics and distribution of billfishes. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972. NOAA Tech. Rep. SSRF-675(2):45-53.

Nishikawa, Y., M. Honma, S. Ueyanagi, and S. Kikawa. 1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956-1981. Bull. Far Seas Res. Lab. S. Series (12), 99 p.

Schaefer, M., G. Broadhead, and C. Orange. 1963. Synopsis on the biology of yellowfin tuna *Thunnus* (Neothunnus) *albacares* (Bonnaterre, 1778 (Pacific Ocean)). *In:* Proc. World Sci. Meeting on the Biology of Tuna and Related Species. FAO Fish Rep. 8(2):538-561.

Shingu, C., P. Tomlinson, and C. Peterson. 1974. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1967-1970. Inter. Am. Trop. Tuna Comm. Bull. 16(2):68-230.

Shiohama, T. 1969. A note on the marlin caught by tuna longline fishery in the eastern Pacific Ocean east of 130°W. Bull. Far Seas Fish. Res. Lab., March 1969(1):5-34.

Shomura, R. (ed.). 1980. Summary report of the billfish stock assessment workshop Pacific resources. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-5, 58 p.

Squire, J. 1987. Striped marlin *(Tetrapturus audax)* migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program. Mar. Fish. Rev. (Mar. Rec. Fisheries and Fishing) 49(2):26-43.

Squire, J. and D. Nielsen. 1983. Results of tagging program to determine migration rates and patterns for black marlin *(Makaira indica)* in the southwest Pacific Ocean. NOAA Tech. Rep., NMFS-SSRF-772, 19 p.

Squire, J. and D. Au. 1990. Management of striped marlin *(Tetrapturus audax)* resources in the northeast Pacific — A case for local depletion and core area management. Current volume.

Suda, A. and M. Schaefer. 1965. General review of the Japanese tuna longline fishery in the eastern tropical Pacific Ocean 1956-1962. Inter-Am. Trop. Tuna Comm. Bull. 9(6):305-462.

Suzuki, Ziro, P. Tomlinson, and M. Honma. 1978. Population structure of Pacific yellowfin tuna. Inter-Am. Trop. Tuna Comm. Bull. 17(5):277-439.

Ueyanagi, Shoji. 1959. Larvae of the striped marlin *(Makaira mitsukurii)* (Jordan and Snyder). Rep. Nankai Reg. Fish. Res. Lab. 11:130-146.

Ueyanagi, Shoji. 1974. A review of the world commercial fisheries for billfishes. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972. NOAA Tech. Rep. SSRF-675(2):1-11.

Ueyanagi, Shoji and P. Wares. 1975. Synopsis of biological data on striped marlin, *Tetrapturus audax* (Philipps), 1887. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972. NOAA Tech. Rep., SSRF-675(3):132-159.

Wares, P. and G. Sakagawa. 1974. Some morphometrics of billfishes from the eastern Pacific Ocean. *In:* R. Shomura and F. Williams (eds.), Proc. Int. Billfish Symp., Kailua-Kona, HI, 9-12 August 1972. NOAA Tech. Rep. SSRF-675(2):107-120.

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Interpreting Long-Term Fish Landings Records: Environment and/or Exploitation?

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ABSTRACT: The California Department of Fish and Game data base of California commercial fish landings for the period 1928 to 1985 has been assembled in computer accessible form at the Pacific Fisheries Environmental Group in Monterey, California. Time series for fishes whose landings are known to vary during periods of ocean warming were compared to time series of sea surface temperature. Expected patterns of variation were confirmed in the seasonal cycle, but were less clear on the interannual scale. When interannual variation was considered, the most serious hindrance to interpretation of the landings series appeared to be the continued reduction of the fish stocks due to commercial exploitation; other factors are discussed. Landings data contain information potentially useful in climatological studies, but problems should be anticipated in their use.

INTRODUCTION

Fish landings data are one of few types of marine biological data that exist for periods of time sufficient for climatological investigations. This report announces the digitization and archiving of 58 years of commercial fish landings data from California Department of Fish and Game (CDF&G) records. It discusses a preliminary investigation into the value of this data set as a source of information on temporal variation in the marine ecological system, and it gives examples of problems encountered in extracting useful information from them.

The approach used here to test the utility of the data set has been to state a well known hypothesis relating landings variability to ocean warming; to test this hypothesis using a subset of the data; and then to examine the results of the test from two points of view. First, how well is the hypothesis demonstrated? Second, identify factors other than the one hypothesized that influence variability in landings.

Previous studies have shown that increased commercial and sport landings of albacore, bonito, barracuda, bluefin tuna, skipjack tuna, swordfish, and white seabass along the California coast vary simultaneously with warming of the coastal waters (Walford, 1931; Hubbs, 1948; Radovich, 1960, 1961, 1975; MacCall et al, 1974; Squire, 1987.) This well established relationship is the known hypothesis to be tested below using the newly archived data. Our results may not be expected to be new, but they will amplify past work and will provide a framework for discussion of some of the problems encountered in the use of landings data.

DATA

The newly archived data series for the 1928 to 1985 period was obtained from the CDF&G. For the years 1928 to 1977, these data are in publications of the CDF&G *Fish Bulletin* series. The data since 1978 have not been published, but corresponding records for 1978 to 1985 were obtained from the Monterey, CA, office of CDF&G. These all have been archived digitally at the Pacific Fisheries Environmental Group for the six California statistical regions shown in Figure 1. This report uses data from the Santa Barbara, Los Angeles, and San Diego statistical regions. The species of fish selected for consideration are commonly known to have their presence and/or levels of abundance related to warming *(op cit)* of the coastal ocean environment.

The Scripps pier temperature data set is one of few environmental time series of length comparable to the fish landings time series. It is used as an index of conditions in the Southern California region (Mooers et al., 1986; Smith and Eppley, 1982; Fiedler, 1984).

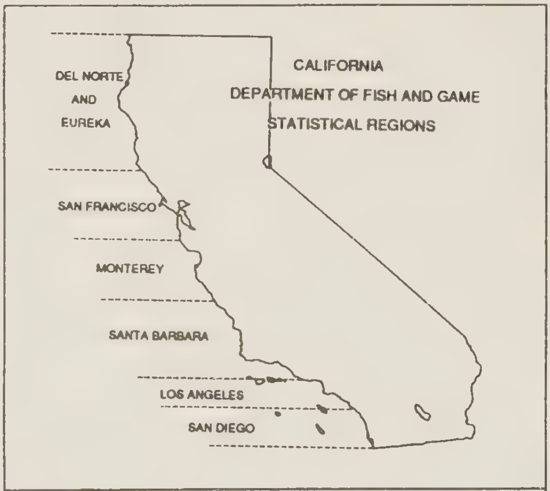

Figure 1. Statistical regions from which landings of commercially caught fishes are reported by California Department of Fish and Game.

In J.L. Betancourt and A.M. MacKay, editors, 1990. Proceedings of the Sixth Annual Pacific Climate (PACLIM) Workshop, March 5-8, 1989: California Department of Water Resources, Interagency Ecological Studies Program Technical Report 23.

PROBLEMS AND EXAMPLES

A representative time series plot of monthly landings (Figure 2) shows that the seasonal cycle is conspicuous, as are interannual variations and multi-year trends in the level of landings.

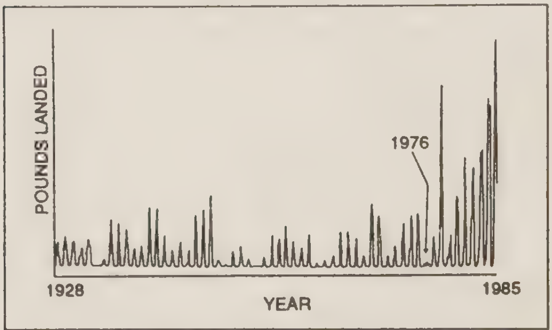

Figure 2. Monthly landings of swordfish at Southern California ports, 1928 to 1985. Note major change in trend at about 1976; see text.

Plots of long-term average monthly landings (annual seasonal cycle) of selected warm - water species (Figure 3) illustrate that albacore, bluefin, skipjack, white seabass, bonito, and swordfish landings peak in August and September (skipjack landings have an additional minor peak in April). Barracuda landings peak in June and July. The principal peaks of landings of all the species except barracuda occur when the Scripps pier SST is at a maximum (last panel, Figure 3). The composited (normalized and summed) long-term monthly mean landings and SST correlate at $r = 0.96$, and all except barracuda are individually correlated at significance levels over 99% (r over 0.69). In terms of seasonality then, the hypothesis that the test species are associated with periods of warm water is well validated by the commercial landings data set. The correlation of $r = 0.96$ shows a close seasonal phase relationship between the warm-water species and the ocean temperature indicator.

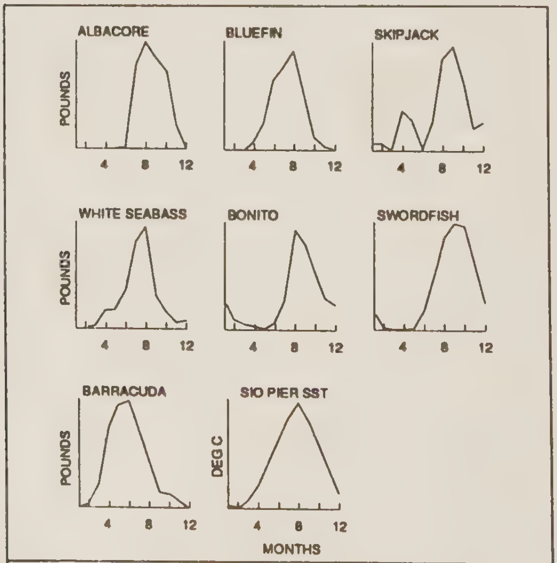

Figure 3. Long-term average monthly landings of warm-water fishes in the Southern California bight. Plots show types of seasonal patterns in landings. Vertical axes are not labeled because each panel is scaled to give the maximum value full scale.

We next made an exploratory test of the interannual relationship between summed annual landings and SST. The annual total landings for the test species were normalized to standard deviation units and summed for each year; the data were combined for all species then were compared to Scripps pier SST. This simple approach of summing the annual landings for each species for each year and correlating this with SST gives a seemingly correct association, $r = 0.61$, between fish landings and warm ocean conditions on the interannual scale (MacCall et al., 1974; Radovich, 1961, 1975). However, the SST time series pattern is dominated by four warm-water periods at 1931, 1941, 1957-60, 1982-84 (see smoothed SST curve, Figure 4), seemingly related to the timing of major warm (El Niño Southern Oscillation, or ENSO) events. And the landings data show trends and shifts in levels that are due to natural and anthropogenic causes. Factors such as these partly obscure the environmental influence on landings and contribute to reducing the effective degrees of freedom (n = 58) by introducing autocorrelation.

When the species are tested individually against SST, it is noted that only skipjack has an r-value comparable to the composite series ($r = 0.51$; Figure 4). Further examination of the individual series shows conspicuous overall trends in all the fish landings time series plots except albacore and skipjack.

The plot of annual albacore landings for the three southern regions may be misleading, because albacore landings distributions change between Southern California waters and the region from Northern California to British Columbia. Albacore apparently enter those northern regions from the west. Thus the plot presented may not reflect the coastwide landings of albacore. The other species appear to enter the Southern California region from the south or southwest.

White seabass landings show a general decline. An exceptional increase in landings occurred during the 1957-59 ENSO event, in which they reached an all time peak of 3.4 million pounds. Increases of lesser magnitudes also occurred at the times of warm events in 1931, 1941 and 1972-73.

Barracuda landings show an even more abrupt decline. Increases in landings, apparently associated with the 1957-59 ENSO event, as well as the prior major event in 1940-41, are evident.

The bluefin tuna landings time series shows noticeable maxima during the 1941 and 1957-59 warm water events.

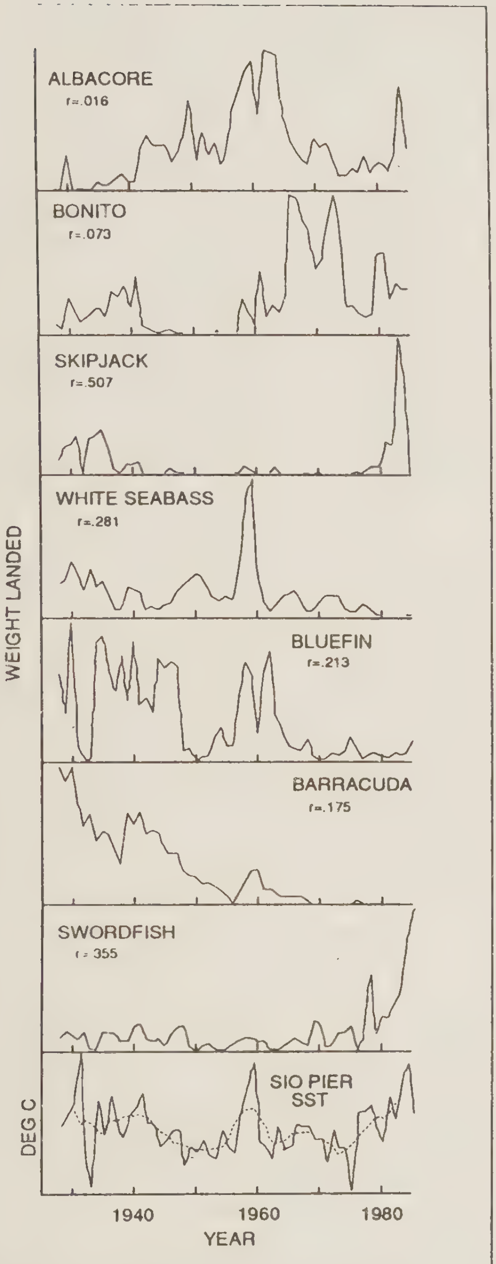

Figure 4. Time series plots of annual landings of warmwater fishes and Scripps pier surface temperature, 1928-1985. Correlation coefficients (*r*) for each species and SST are given in each panel. Vertical axes are not labeled because each panel is scaled to give the maximum weight landed full scale. Dashed line in SST panel is 5-year running mean.

COMMENTS AND DISCUSSION

Commercial fish landings statistics are one of only few kinds of data on biological variation in the ocean available over periods of time of sufficient length to permit their use in bioclimatological investigations. To make good use of these data, however, requires considerably more information. Data concerning any resource highly impacted by man's economic or other activities are likely to have variability in amplitudes and frequencies that are greater than those induced by non-anthropogenic factors. This appears to be demonstrated by the commercial fish landing data.

Bluefin tuna and barracuda have generally declined in abundance over the 58-year period studied. Commercial fishing probably has been an important factor contributing to this decline. Reduction in stock size may have occurred during periods of increased availability to the commercial fisheries.

Episodic increases in landings followed by declines may mean that the total populations were more accessible to fishing during warming events, but not necessarily more abundant at those times. Landings for barracuda and white seabass declined rapidly after reaching peaks occurring simultaneously with warmings (Figure 4). This may explain why the association between the landings of the fishes studied herein and warm water is not as evident during the warm events that occurred since 1959; there may not have been sufficient stocks size for an expression of the environmental relationship to be evident.

There has been an increase in swordfish landings (Figures 2 and 4) that began simultaneously with the onset of an ocean climate shift in 1976 (Norton et al., 1985; PACLIM Abstracts, 1986, 1987, 1988). Because the swordfish market demand usually exceeds supply, all fish landed can be sold. In the mid-1970s it was discovered that swordfish could be caught more easily with gillnets than by the traditional harpoon method (Bedford and Hagerman, 1983). The catch by harpooning has remained about constant (*ibid*), but introduction of the new gillnet gear made it possible to extend the fishery into waters that had been unsuitable for harpooning. This expanded the area subject to fishing and also extended the time fish were available to exploitation. The result has been a major increase in landings that occurred simultaneously with a major environmental shift. The connection between ocean climate (SST) and catch is, at this point, unclear because the new fishing methods were introduced coincidentally with the onset of the environmental change.

Various methods for combining data from different sources are being developed. Independent scientific surveys of adults may be used to determine species abundance. This approach has been used for sablefish, rockfish, and some species of wet fish. Other surveys might monitor changes in numbers of eggs, larvae and juveniles. From these surveys, fisheries independent estimates of stock abundance may be possible.

Combination of sport and commercial catch records may help to interpret trends. These two data sets are controlled by somewhat different variables. Sportfishing is not for profit, whereas commercial fishing is profit driven; but a certain level of success is necessary in either case.

In a recent report to the Pacific Fisheries Management Council, Methot and Hightower (1988) combined information from scientific surveys and tagging experiments to arrive at estimates of current and previous sablefish stock sizes.

We have explored the climatological variations in the relationship of SST and commercial fish landings. The expected linkage seems confirmed; but we demonstrated that users of landings data should be aware of the presence and possible effects of other factors on landings variability. These include:

- Autocorrelation introduced by extreme environmental events,
- Depletion of the species,
- Fishing gear changes,
- Merchandising demand factors,
- Availability of market replacement species, etc.

SUMMARY

- Commercial fish landing data compiled by the CDF&G have been refined into a uniform, computerized data base at the PFEG.
- These data have been tested with a commonly accepted hypothesis relating ocean warming and landings variability. The data strongly support the hypothesis on the inter-monthly or seasonal scale, but the relationship is less decisive on the interannual scale. That linkage is partially obscured by the interplay of numerous factors.
- Declines in fish landings over time, as a possible result of high exploitation during warm water periods and high abundance, is thought to be a major factor which confuses simple interpretation of these commercial landings data.
- Other data sources and data processing techniques will be used to obtain additional information on the marine ecosystem from the commercial fish landings data set.

REFERENCES

Bakun, A., and Parrish, R., 1980, Environmental inputs to fishery population models for eastern boundary current regions, in Sharp, G., Ed., Workshop on the effects of environmental variation on the survival of larval pelagic fishes: Paris, Intergovernmental Oceanographic Commission, UNESCO, IOC Workshop Report, v.28, p.67-104.

Bedford, D.W., and Hagerman, F.B., 1983, The billfish fishery of the California Current: CalCOFI Report, v.XXIV, p.7078.

Cayan, D.R., McLain, D.R., and Nichols, W.D., In prep., The PACLIM Monthly Time Series Atlas: U.S. Geological Survey Open File Report.

Fiedler, Paul C., 1984, Effects of El Niño on the northern anchovy: California Cooperative Fishery Investigation Report (CalCOFI), v.25, p.53-58.

Hubbs, C.L., 1948, Changes in the fish fauna of western North America correlated with changes in ocean temperature: Journal of Marine Resources, v.7, p.459-482.

Jordan R.S., 1983, Variabilidad de los recursos pelagicos en el Pacifico sudeste, in Proceedings of the expert consultation to examine changes in abundance and species composition of neuritic fish resources: FAO Fisheries Report No. 291, v.2, p.113-129.

MacCall, A.D., Stauffer, G.D., and Troadec, J.P., 1974, Stock assessments of Southern California recreational and commercial marine fisheries: U.S. Department of Commerce, NOAA, NMFS, Southwest Fisheries Center, Admin. Report LJ-74-24, 144p.

Mendelssohn, R., and Cury, P., 1987, Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions: Canadian Journal of Fish. Aquatic Sciences, v.44, p.408-421.

Methot, Richard, and Hightower, Joseph, 1988, Status of the Washington - Oregon - California sablefish stock in 1988 (submitted to the Pacific Fisheries Management Council, Portland, Oregon, October 1988), Northwest and Alaska Fishery Center, National Marine Fisheries Service, 7600 Sand Point Way, NE, Seattle, WA 98115, and Southwest Fisheries Center, Tiburon Laboratory, 3150 Paradise Drive, Tiburon, CA 94920.

Mooers, Christopher N.K., Peterson, D.H., and Cayan, Daniel R., 1986, The Pacific Climate Workshops: EOS - Transactions, American Geophysical Union, v.67, no.52, p.1404-1405.

Murphy, G.I., 1966, Population biology of the Pacific sardine *(Sardinops caerulea)*: Proceedings California Academy of Sciences, v.34, no.1, p.1-84.

Norton, J., McLain, D., Brainard, R., and Husby, D., 1985, The 1982-83 El Niño event off Baja and Alta California and its climate context, in Wooster, W., and Fluharty, D., Eds., El Niño North: Seattle, Washington Sea Grant Program, University of Washington, p.44-72.

Norton, J., 1987, Ocean climate influences on groundfish recruitment in the California current, in Proceedings of the International Rockfish Symposium, October 20-22, 1986: Fairbanks, Alaska Sea Grant College Program, University of Alaska.

Parrish, R., Nelson, C., and Bakun, A., 1981, Transport mechanisms and reproductive success of fishes in the California current: Biology of Oceanography, v.1, no.2, p.175-203.

Radovich, J., 1975, Water temperature and fish distribution: An epilogue to the warm water years, in Rec. Proceedings of 13th Pacific Science Congress, Aug. 18-30, 1975: Vancouver, University of BC, v.1, p.264-265.

_______, 1961, Relationship of some marine organisms of the northeast Pacific to water temperatures: California Department of Fish and Game, Fish Bulletin 112, 62p.

_______,1960, Redistribution of fishes in the eastern north Pacific Ocean in 1957 and 1958, in California Coop. Oceanic Fish. Investigation Report 7, p.163-171.

Smith, Paul E., and Eppley, R.W., 1982, Primary production and the anchovy population in the Southern California Bight: Comparison of time series: Limnology of Oceanography, p.27, 1-17.

Squire, J.L., 1987, Relation of sea surface temperature changes during the 1983 El Niño to the geographical distribution of some important recreational pelagic species and their catch temperature parameters: Marine Fisheries Review, v.49, no.2, p.44-57.

Walford, L.A., 1931, Northward occurrence of southern fish off San Pedro in 1931: California Fish Game 17, p.401-405.

Wooster, W.S., and Fluharty, D.L., Editors, 1985, El Niño North, Niño effects in the eastern subartic Pacific Ocean: Seattle, Washington Sea Grant Program, University of Washington.

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A new sound from a stranded pygmy sperm whale

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Introduction

The pygmy sperm whale (*Kogia breviceps*) has a cosmopolitan distribution in temperate, subtropical and tropical waters of the Atlantic and Pacific oceans (Leatherwood and Reeves, 1983). In the Pacific, it most commonly strands in southeastern Australia, New Zealand, the west coast of North America from Washington state to the Gulf of California, and Japan. Members of this species are rarely seen at sea; they are most commonly observed as individuals or in small groups (Walker, 1975). They are not notably soniferous. Watkins and Wartzok (1985) report only pulsed sounds for this species. Using a towed array of hydrophones, a *Kogia* was followed in the eastern tropical Pacific for about 30 minutes, but no distinguishable sounds were heard (Thomas, unpublished data).

Airborne recordings by Caldwell *et al.* (1966) and underwater recordings by Caldwell and Caldwell (1987) of *Kogia breviceps* recovered from strandings showed low-amplitude echolocation-like clicks of varying repetition rates with peak frequencies below 13 kHz. These authors note the importance of recording sounds of stranded cetaceans as a means of documenting their repertoire, especially in this uncommon species. We had the opportunity to make underwater recordings of a stranded *Kogia breviceps* that beached on Oahu and to further document other aspects of this species by videotape recordings. We advocate that simultaneous video and audio records be made on stranded marine mammals to provide a permanent record of many aspects of the animal's behaviour and appearance.

Species account

On the morning of 14 August 1988 a pygmy sperm whale (*Kogia breviceps*) was found stranded at Punalu'u beach on the northeast shore of the island of Oahu, Hawaii. The adult female was transported to Sea Life Park and housed in a large circular pool. She weighed 364.8 kg and was 269 cm long. She had a few scars, and her general appearance was good. She swam slowly around the pool without listing. Her body shape was broad, and a pregnancy was suspected. The whale expired late in the afternoon of 15 August and the necropsy later showed a near-term fetus.

Methods

During the afternoon of 15 August, we made simultaneous video and audio tape recordings of the *Kogia* swimming around the pool. Initial listening indicated that the whale generally was not vocal. It occasionally produced a low-frequency, low-amplitude sound of short duration, but no echolocation-clicks. We made a video tape using a video camera/recorder (Sears model 42850 HQ) with a half-inch VHS format. Underwater recordings were made with a calibrated Gould CH-17 hydrophone, which had been modified to be flat (±3 dB) up to 18 kHz. The output

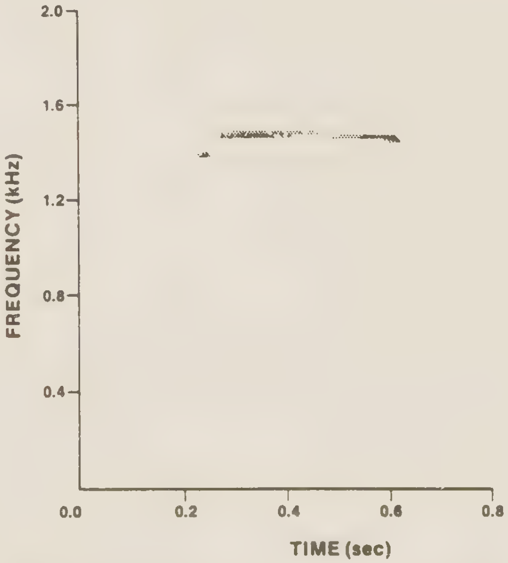

Figure 1. A representation sonogram of a cry from a pygmy sperm whale.

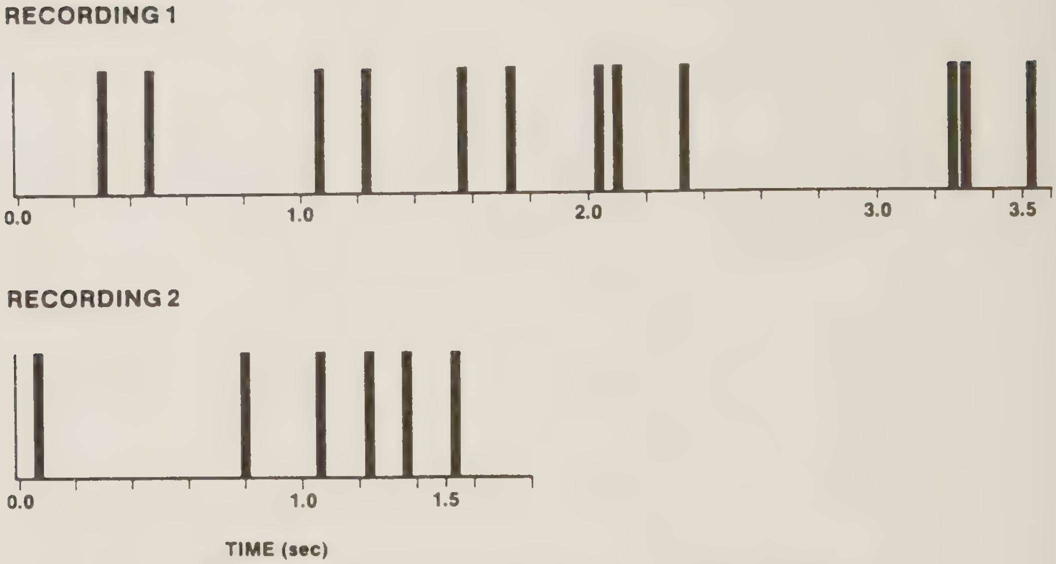

Figure 2. Time-line of cries during the two most active recording periods.

of the hydrophone was passed to a Hewlett Packard amplifier bank (flat from 0 to 300 kHz) and then simultaneously passed to the video camera and a Marantz PMD 430 cassette recorder (frequency response 35 Hz to 15 kHz ± 3 dB). Recordings were made opportunistically over a 2-hour period.

All sounds on the cassette tape were examined using the Uniscan II spectrum analyzer. Coordination of the counters on the video tape player and cassette player allowed us to select the loudest calls produced with a direct orientation to the hydrophone for detailed spectral analysis. We transcribed the temporal sequence of the sound using a digital stop watch.

A review of the video tape allowed us to examine some of the whale's diagnostic characteristics and verify the species of *Kogia*.

Results and Discussion

As far as we know, this is the only synchronized video and audio recording of this species. On retrospective examination, many types of data can be gleaned from a video tape that could not be tracked at the time of data collection.

Based on the small dorsal fin located posterior to the center of the back, the presence of 11 pairs of lower teeth, the absence of upper teeth, and the absence of ventral throat grooves described by Handley (1966), we diagnosed this whale to be a *Kogia breviceps*.

We recorded no echolocation-type clicks as reported by Caldwell and Caldwell (1987). However, we clearly detected a short duration (0.42 sec) ascending sweep or 'cry'. This 'cry' may have been a distress call. Eighteen moderately stereotypic, good quality cries were examined. Figure 1 shows a typical cry with a start frequency of 1.36 kHz and an end frequency of 1.48 kHz. The sounds were heard singly, or in pairs. Figure 2 shows the time-line or sequence of these cries during the two most active recordings.

We advocate that a simultaneous video/audio tape recording of stranded animals provides a wealth of information about the individual and sometimes an unusual species. This permanent record can be viewed by anatomists, behaviorists, taxonomists, and physiologists in retrospect to retrieve pertinent information. The tapes also may provide a valuable training tool for stranding network team members.

Acknowledgements

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Literature Cited

Caldwell, D. K. & Caldwell, M. C. (1987). Underwater echolocation-type clicks by captive stranded pygmy sperm whales, *Kogia breviceps*. Abstracts, Seventh Biennial Conference on the Biology of Marine Mammals, Miami, Florida, Dec. 5–9, 1987, p. 8.

Caldwell, D. K., Prescott, J. H. & Caldwell, M. C. (1966). Production of pulsed sounds by the pygmy sperm whale, *Kogia breviceps*. Bulletin Southern California Academy of Science. **65(4):** 245–248.

Handley, C. D. (1966). A synopsis of the genus *Kogia* (pygmy sperm whales). *In* Norris, K. S. ed., *Whales dolphins and porpoises*, University of California Press, Berkeley, CA.

Leatherwood, S. & Reeves, R. R. (1983). The Sierra Club Handbook of Whales and Dolphins. Sierra Club Books, San Francisco. pp. 90–93.

Walker, E. P. (1975). Mammals of the World. Vol. II, Third Edition. The John Hopkins University Press, Baltimore. pp. 1098–1101.

Watkins, W. A. & Wartzok, D. (1985). Sensory biophysics of marine mammals. Marine Mammal Science. **1(3):** 219–260.

9064

THE MARKET FOR FISH MEAL AND OIL IN THE UNITED STATES: 1960–1988 AND FUTURE PROSPECTS

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ABSTRACT

Fish meal is used in the United States largely as a high-protein ingredient in poultry feed. Prices of domestic fish meal are determined by world market conditions for fish meal as well as other oil meals. Faced with limited fish meal supplies and little control over prices, the U.S. poultry industry has substituted other ingredients and made use of technological advances to satisfy the nation's growing demand for table birds.

A number of factors have been identified that may significantly affect future demand, supply, and prices of fish meal and oil, both in the United States and abroad. These include (1) increases in world aquaculture production, (2) possible development of a domestic market for hydrogenated fish oil, (3) recent changes in the Alaska pollock fishery, (4) efforts to develop marketable products for direct human consumption from reduction species, and (5) the status of the Japanese and South American sardine fisheries.

RESUMEN

La harina de pescado es un ingrediente de alto contenido proteico utilizado corrientemente en la alimentación de aves de corral en los Estados Unidos de Norteamérica. El mercado mundial determina el precio de la harina, como así también el de otras harinas de orujo. Ante el problema de un limitado abastecimiento de harina de pescado y un reducido control en los precios, la industria de la pollería se vió obligada a sustituír otros ingredientes y hacer uso de los avances tecnológicos con el fin de satisfacer la creciente demanda de estas aves de corral.

Se han identificado un número de factores que pueden afectar significativamente la futura demanda, el abastecimiento y el precio de la harina de pescado y otros aceites, tanto en los Estados Unidos como en el exterior, a saber: (1) el aumento en la producción de las piscifactorías, (2) el posible desarrollo de un mercado doméstico de aceite de pescado hidrogenado, (3) los cambios recientes en la pesquería del bacalao de Alaska, (4) los esfuerzos para desarrollar productos de consumo directo por el ser humano, y por último (5) el estado de las pesquerías en el Japón y en Sudamérica.

INTRODUCTION

The fish meal and oil industry began in the nineteenth century in northern Europe and North America. The oil was manufactured from surplus fish caught in the herring fishery, and was used to tan leather and as an ingredient in products such as soap. The residue was originally used as fertilizer. However, since the turn of this century, the use of fish for fertilizer has diminished considerably because increasing amounts have been diverted to the production of fish meal (FAO 1986).

The fish meal production process, which is known as reduction, involves cooking the fish, removing the water and oil from it, drying the solid material left behind, and grinding it into a meal. Fish meal is used in the United States largely as a high-protein ingredient in poultry feed. It is also used in feeds for pigs, farmed fish, fur-producing animals, laboratory animals, and household pets.

The oil that is removed in the reduction process is marketed as an ingredient for industrial products (such as paints and lubricants) and foods (such as margarines and shortenings). Most of the fish oil produced in the United States has historically been exported to Europe for use in margarines. Until very recently, the U.S. Food and Drug Administration did not allow the use of fish oil in products for domestic human consumption.

Approximately one metric ton (MT) of fish meal is produced from each 4–5 MT of fish harvested. The oil yield is more variable and depends on the species and the time of year when the fish are caught (Vondruska 1980). For example, the oil content of northern anchovy is low during the winter and spring spawning period, and highest in late summer (Lasker and Smith 1977). The wholesale value of U.S. fish meal production has historically exceeded the value of oil production by a factor of two to four (table 1).

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TABLE 1

Quantity and Value of Fish Meal and Oil Produced in the United States

	Production quantity (1000's of metric tons)		Value (millions of dollars)	
Year	Fish meal	Fish oil	Fish meal	Fish oil
1960	263.2	94.8	25.3	13.0
1961	282.4	117.1	31.9	14.3
1962	283.3	113.4	35.6	11.0
1963	232.2	84.3	30.2	10.9
1964	213.5	81.7	28.0	13.3
1965	230.5	88.7	35.7	14.9
1966	203.4	74.7	32.3	12.5
1967	191.6	55.5	26.0	6.1
1968	213.3	79.0	30.3	7.3
1969	229.2	77.0	39.8	9.3
1970	244.2	93.5	46.4	18.2
1971	265.6	120.4	44.5	20.8
1972	259.0	85.5	48.3	13.1
1973	253.2	101.9	119.1	25.6
1974	264.6	107.9	83.5	49.2
1975	253.4	111.4	64.6	32.6
1976	271.3	92.8	95.7	31.2
1977	248.4	60.7	96.5	28.4
1978	320.9	134.4	120.2	60.7
1979	329.2	121.4	133.3	54.1
1980	322.3	141.8	132.9	57.9
1981	281.3	83.6	117.6	33.1
1982	330.4	157.6	121.2	53.6
1983	339.0	181.1	129.1	66.8
1984	334.7	169.1	112.6	61.0
1985	319.6	129.3	83.1	41.9
1986	308.1	152.8	82.4	43.7
1987	349.6	135.4	120.9	35.5
1988	283.5	101.9	129.2	43.6

References: U.S. Department of the Interior 1960–1970; U.S. Department of Commerce 1971–1988.

Fish and shellfish landed commercially in the United States are used for human consumption and industrial products. Over 85% of industrial use is attributable to reduction; the remainder consists of bait and animal food. Since 1960, industrial uses have accounted for 36%–53% of total landings but only 4%–11% of total ex-vessel revenues on an annual basis (table 2). Reduction landings tend to be large in quantity but low in value relative to landings used for direct human consumption.

SUPPLY

Production

The species used for reduction are small, oily, pelagic fishes that are not marketable in large quantities for human consumption. In the United States, these include northern anchovy *(Engraulis mordax)* on the Pacific Coast and menhaden *(Brevoortia tyrannus* and *B. patronus)* on the Atlantic and Gulf coasts. A substantial reduction fishery once existed in California for Pacific sardine *(Sardinops sagax)*, but the fishery collapsed in the early 1950s (Radovich 1981). The state of California lifted its moratorium on sardine landings in 1986, but so far has allowed modest harvests to be taken for nonreduction uses only.

Although most fish meal is produced from whole fish, about 10% is produced from the by-catches and byproducts of other fisheries. Examples are tuna-mackerel and pollock meals, which are produced from the scraps remaining after these species are processed into other market products.

As indicated in table 3, U.S. fish meal production ranged from 200 to 350 thousand MT per year from 1960 through 1988. Before 1982, menhaden meal constituted 55%–80% of annual production. Since 1982, menhaden's share has been even higher, averaging 85% of total production. Tuna-mackerel meal contributes 20,000–45,000 MT per year.

Anchovy meal production peaked in 1975 at 25,100 MT, when its share of total production was 10%. However, meal production from this species has been much lower in most other years and has been negligible since 1983, largely because of economic factors rather than low abundance. From 1983 through 1988 the fish meal price ranged from $240 to $440 per MT, and the ex-vessel price received by the menhaden fleet ranged from $80 to $115 per MT. However, for reasons that are not clear, the ex-vessel anchovy price offered by California processors has remained at record low levels (below $35 per MT). As a result, the California reduction fleet has not found it profitable to target on anchovy and has directed increasing amounts of effort to more lucrative species such as mackerel, tuna, and squid (Thomson et al. 1989).

Imports and Exports

Figure 1 describes the contributions of Peru and Chile to world exports of fish meal. From 1960 to 1972 Peruvian anchoveta *(Engraulis ringens)* accounted for 50%–63% of all the fish meal traded in international markets. A combination of overfishing and poor recruitment led to the collapse of the fishery during the 1972–73 El Niño (Glantz 1979). The recovery of the fishery has enabled Peru to significantly increase its exports in the 1980s, though not to the high levels of the 1960s and early 1970s. Chile's fish meal exports began to increase in the early 1970s, as a result of its developing sardine *(Sardinops sagax)* and jack mackerel *(Trachurus murphyi)* fisheries. Since 1980 Chile's exports have exceeded Peru's.

TABLE 2
U.S. Commercial Finfish and Shellfish Landings and Ex-Vessel Value (Millions of Dollars) by Disposition of Catch

Year	Human food		Industrial use[b]		Total	
	Landings[a]	Value	Landings	Value	Landings	Value
1960	1133.1	—	1108.6	—	2241.7	354
1961	1129.5	—	1223.4	—	2352.8	362
1962	1152.1	—	1276.4	—	2428.6	396
1963	1159.4	—	1039.2	—	2198.6	377
1964	1132.6	—	927.2	—	2059.8	389
1965	1173.6	408	993.2	29	2166.8	446
1966	1166.9	437	813.5	24	1980.4	472
1967	1073.9	414	765.3	17	1839.1	440
1968	1064.1	468	822.8	29	1887.0	497
1969	1052.8	492	914.5	35	1967.3	527
1970	1150.8	565	1079.6	48	2230.3	613
1971	1107.2	604	1168.9	47	2276.1	651
1972	1104.5	702	1075.3	46	2180.0	748
1973	1087.7	836	1115.8	101	2203.6	937
1974	1132.2	844	1120.8	88	2253.0	932
1975	1118.1	904	1094.1	73	2212.2	977
1976	1258.7	1257	1185.2	92	2444.0	1349
1977	1339.0	1440	1051.9	114	2390.9	1554
1978	1441.1	1733	1293.2	121	2734.3	1854
1979	1505.0	2093	1337.7	141	2842.7	2234
1980	1657.4	2092	1282.8	145	2940.2	2237
1981	1608.9	2277	1102.2	111	2711.1	2388
1982	1490.1	2247	1398.0	143	2888.1	2390
1983	1468.7	2203	1452.0	152	2920.7	2355
1984	1505.9	2206	1414.3	144	2920.3	2350
1985	1494.1	2198	1344.5	128	2838.6	2326
1986	1539.1	2641	1196.6	122	2735.6	2763
1987	1789.9	2979	1338.1	136	3128.0	3115
1988	2081.1	3362	1181.2	158	3262.3	3520

[a] Thousands of metric tons, round weight; excludes weight of mollusk shells.
[b] Over 85% processed into meal, oil, and solubles. The remainder is used for shell products, bait, and animal food.
References: U.S. Department of the Interior 1960–1970; U.S. Department of Commerce 1971–1988.

The two countries together account for 40%–50% of world fish meal exports in the 1980s.

U.S. imports of fish meal have tended to follow the worldwide pattern of availability. As indicated in table 4, Peru provided us with 52%–90% of our imported supplies from 1960 through 1972. Peruvian imports declined significantly after the collapse of the anchoveta fishery, and the resulting void was not substantially filled by anyone else until the mid-1980s. In recent years, Chile has emerged as our major foreign supplier. We also import a modest but fairly steady amount of meal (averaging about 30,000 MT annually) from Canada, and smaller and more variable amounts from miscellaneous other countries.

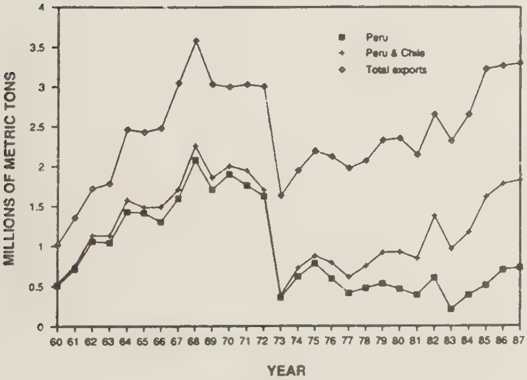

Figure 1. Fish meal exports by Peru, Chile, and all countries, 1960–87.

Up until 1970, U.S. fish meal exports were negligible and tended to be disregarded in published statistics. Exports have fluctuated widely from 4,300 to 77,400 MT during 1970–88. Exports exceeded imports in 1978, 1980, and 1983 (table 4).

Total fish meal supply (i.e., production plus imports minus exports) has declined somewhat in the post-1972 period relative to earlier years (figure 2). The variability in supply closely parallels the variability in net imports (i.e., imports minus exports). Domestic production (depicted by the difference between supply and net imports) has been much more stable by comparison.

TABLE 3

Fish Meal Production in the United States by Species (Thousands of Metric Tons)

Year	Menhaden	Tuna-Mack	Anchovy	Other	Total
1960	198.1	24.0	0.0	41.0	263.2
1961	224.6	19.2	0.0	38.6	282.4
1962	217.5	24.1	0.0	41.7	283.3
1963	167.1	24.5	0.0	40.6	232.2
1964	145.4	19.1	0.0	48.9	213.5
1965	159.7	23.0	0.0	47.8	230.5
1966	122.5	23.0	4.1	53.9	203.4
1967	108.0	23.1	5.1	55.3	191.6
1968	129.9	26.1	2.5	54.7	213.3
1969	144.7	24.4	10.3	49.8	229.2
1970	171.1	24.2	14.7	34.2	244.2
1971	200.5	26.6	7.0	31.6	265.6
1972	175.6	39.2	10.1	34.1	259.0
1973	171.3	39.6	20.0	22.4	253.2
1974	185.0	43.7	12.8	23.1	264.6
1975	173.6	33.7	25.1	20.9	253.4
1976	192.9	36.4	20.1	21.9	271.3
1977	175.4	36.1	17.3	19.6	248.4
1978	250.8	45.9	1.9	22.2	320.9
1979	254.7	43.0	9.0	22.5	329.2
1980	246.0	42.6	7.1	26.6	322.3
1981	209.4	42.8	9.3	19.9	281.3
1982	273.9	32.1	7.3	17.1	330.4
1983	286.6	37.8	0.5	14.2	339.0
1984	285.7	33.7	0.0	15.3	334.7
1985	279.0	31.3	0.0	9.3	319.6
1986	268.8	33.7	0.0	5.6	308.1
1987	303.4	38.3	0.0	8.0	349.6
1988	228.9	34.5	0.0	20.1	283.5

References: U.S. Department of the Interior 1960–1970; U.S. Department of Commerce 1971–1988.

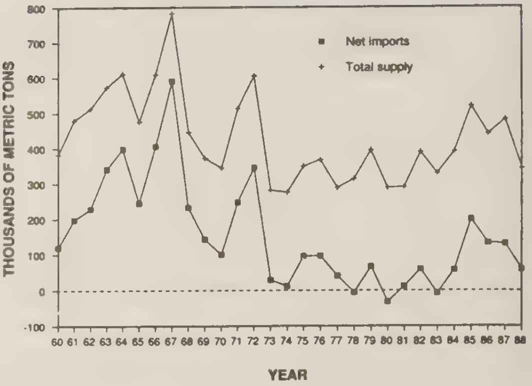

Figure 2. U.S. supply and net imports of fish meal, 1960–88.

PRICES

High-protein oil meals, like fish meal, are traded in a very competitive international market. The soybean meal price is generally considered to be a leading indicator for fish meal and other oil meal prices. Figure 3 is a graph of U.S. soybean meal and menhaden meal prices, both corrected for inflation to 1988 dollars. The prices are highly correlated, with the price differential largely attributable to the difference in protein content.

TABLE 4

U.S. Fish Meal Imports, Exports, and Net Imports (Thousands of Metric Tons)

	Imports by country of origin					Exports	Net imports
Year	Peru	Chile	Canada	Other	Total		
1960	61.7	19.1	28.1	10.8	119.7	—	119.7
1961	137.3	11.0	34.7	14.6	197.6	—	197.6
1962	168.9	8.3	38.8	12.9	228.9	—	228.9
1963	258.9	21.4	46.3	14.8	341.4	—	341.4
1964	315.7	11.7	49.7	21.2	398.3	—	398.3
1965	190.3	5.2	39.7	10.4	245.6	—	245.6
1966	250.9	81.1	39.6	34.6	406.2	—	406.2
1967	401.4	37.1	42.3	110.2	591.0	—	591.0
1968	182.6	18.3	13.0	19.2	233.1	—	233.1
1969	99.8	19.6	19.2	4.7	143.3	—	143.3
1970	73.9	6.4	22.4	2.4	105.1	4.3	100.8
1971	181.1	0.0	52.3	23.5	256.9	9.2	247.7
1972	319.5	0.0	25.0	11.1	355.6	9.4	346.2
1973	37.9	0.0	22.3	1.9	62.1	33.3	28.8
1974	26.7	0.0	27.5	7.8	62.0	50.3	11.7
1975	68.5	7.0	30.8	1.1	107.4	10.7	96.7
1976	72.0	0.0	30.8	24.6	127.4	30.0	97.4
1977	14.2	2.0	22.5	35.2	73.9	32.7	41.2
1978	6.0	0.0	29.7	4.1	39.8	46.0	−6.2
1979	25.6	7.5	24.7	23.5	81.3	14.2	67.1
1980	6.0	0.0	22.0	16.9	44.9	77.4	−32.5
1981	0.0	24.3	22.0	7.6	53.9	42.6	11.3
1982	4.7	42.8	22.4	6.6	76.5	16.2	60.3
1983	6.5	23.4	20.9	10.8	61.6	70.2	−8.6
1984	0.0	43.5	21.4	10.8	75.7	18.3	57.4
1985	0.0	131.6	23.0	77.0	231.6	31.4	200.2
1986	12.4	105.6	16.3	33.8	168.1	34.9	133.2
1987	27.9	94.4	29.2	27.1	178.6	46.9	131.7
1988	46.7	25.4	32.0	16.3	120.4	68.0[a]	59.4

[a] Error in published statistics corrected per Steve Koplin, NMFS, Washington, D.C., pers. comm.

References: U.S. Department of the Interior 1960–1970; U.S. Department of Commerce 1971–1988.

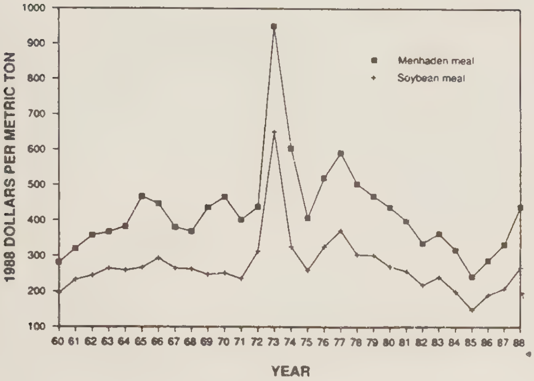

Figure 3. U.S. menhaden meal price (60% protein, bulk, f.o.b., East Coast/ Gulf plants) and soybean meal price (50% protein, bulk, Decatur, Illinois) in 1988 dollars, 1960–88.

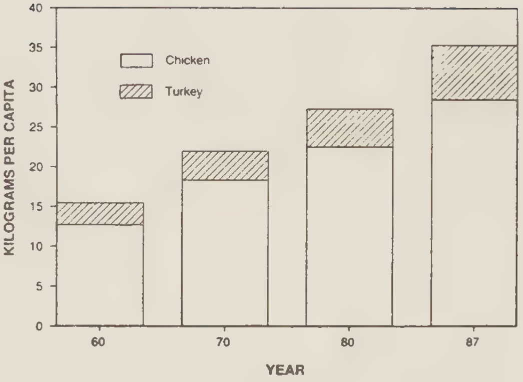

Figure 4. U.S. per capita consumption of chickens and turkeys in 1960, 1970, 1980, and 1987.

A notable feature of the graph is the 1973 price increase, which resulted from a serious worldwide shortage of oil meals. Several factors contributed to this shortage, including (1) major failures of oil meal crops around the world, (2) increases in fuel-related production costs due to the Arab oil embargo, and (3) the collapse of the Peruvian anchoveta fishery.

DEMAND

Demand for Poultry Products

In the years since World War II, the average American diet has shifted away from grain products in favor of more animal protein. This increased demand for protein is partially reflected in the shift from farm production of chickens to the factory-style mass production of commercial broilers that we see today. Approximately 80% of the fish meal consumed in the United States is used as an ingredient in poultry feed (Vondruska 1980). The final demand for poultry products is an indicator of poultry feed usage and the demand for fish meal.

U.S. egg production increased steadily from 61 billion eggs in 1960 to 70 billion eggs in 1967. In the twenty years since 1967, annual egg production has not exceeded the 1967 production level. This leveling of production is due to two offsetting factors: (1) a decline in per capita egg consumption, and (2) an increase in population. Because of increased productivity per layer, the stock of laying hens has declined slightly from 295 million hens in 1960 to 280 millions hens in 1987 (U.S. Department of Agriculture 1960–1988; Rogers 1978). These trends suggest that total feed usage by laying hens has not changed significantly since 1960.

The situation with regard to table birds is quite different (figure 4). Poultry consumption, measured in ready-to-cook weight, has more than doubled from 15.5 kilograms (kg) per person in 1960 to 35.3 kg in 1987. This change, compounded by the increase in population over this same period, has resulted in a dramatic increase in poultry production. Table birds slaughtered under federal inspection increased almost fourfold from 3.1 million MT (live weight) in 1960 to 12.2 million MT in 1987 (U.S. Department of Agriculture 1960–1988).

Accommodation of Poultry Industry to Limited Fish Meal Supplies

The large increase in poultry production has not been accompanied by a commensurate increase in fish meal usage. The poultry industry has accommodated itself to limited fish meal supplies by substituting other ingredients in poultry feed mixes, and by making technological changes to promote rapid growth of chicks.

Over 70% of the cost of producing chickens and turkeys, excluding processing and marketing costs, consists of feed (Vondruska 1980). As a result, small changes in feed prices can have a major effect on total costs. U.S. poultry feed mixers are very sophisticated in their use of linear programming techniques to determine least-cost combinations of ingredients (Hansen 1981/1982). They are also very quick to change feed composition in response to changes in prices (Huppert 1980; Thomson 1984).

The role of fish meal in these linear programming models is best understood by examining its nutritional contribution to poultry feed. All fish meal contains lysine and methionine, which are essential for the development and rapid growth of chicks. These amino acids are not found in grain meals, except for soybean meal, which contains high levels of lysine. Lysine and methionine are also available in synthetic form. The synthetic versions can be used to obtain a proper amino acid balance in feed mixes that do not contain fish meal (Titus and Fritz 1971; Vondruska 1980; Hansen 1981/1982).

Including fish meal in the diet of laying hens reduces mortality by retarding the accumulation of fat in their livers (Ralph Ernst, USDA/UC Cooperative Extension, Oakland, Calif., pers. comm.). Fish meal also produces a significant growth response in table birds. Nutritional requirements for table birds depend upon a bird's stage of growth, so feed composition varies accordingly. For chickens and turkeys, the maximum inclusion rate for fish meal is about 8%–9% for starter rations and 7% for grower rations. Higher rates than this tend to give a "fishy" flavor to the final product. Desirable minimum inclusion rates are 1%–2% for starter rations and 0%–1% for grower rations (Vondruska 1980).

Thus, one way that feed mixers have been able to satisfy the increased demand for poultry feed in spite of having smaller amounts of fish meal has been by substituting other ingredients. For table birds, they have reduced fish meal from maximum to minimum recommended levels in starter rations and eliminated fish meal entirely from grower rations. They have also largely eliminated fish meal from layer rations (Ralph Ernst, USDA/UC Cooperative Extension, Oakland, Calif., pers. comm.). These changes are consistent with Kolhonen's (1974) prediction that, "In the long run fish meal will be used as a unique small-quantity ingredient in high-quality feeds rather than as a high-amount protein source."

Fish meal use has also been reduced by technological improvements resulting in shorter time to market for chickens and turkeys. In 1960 it took approximately nine weeks to bring a three-pound broiler to market; today it takes six weeks (Ralph Ernst, USDA/UC Cooperative Extension, Oakland, Calif., pers. comm.). As a result, feed requirements (including fish meal requirements) per bird have declined.

FUTURE TRENDS

Aquaculture Demand for Fish Meal

Aquaculture production in the United States almost tripled from 1980 to 1985 (table 5). World production has also increased dramatically, from 4.6 million MT in 1975 to 8.9 million MT in 1985 (table 6). Currently about 10% of the world's fish meal production is used to feed farm-raised finfish and shellfish (FAO 1989). By one estimate (Rhodes 1988), world aquaculture production will reach 22 million MT by the year 2000 and account for about 25% of the world's aquatic harvest. This and other similar projections suggest a long-term increase in demand for fish meal in aquaculture.

TABLE 5

U.S. Aquaculture Production, 1980 and 1985, by Species Group (Metric Tons)

Species group	1980	1985
Catfish	34,855	123,344
Salmon	3,455	38,320
Crawfish	10.849	29,545
Trout	21,836	23,000
Baitfish	10,000	11,276
Oysters	10,755	10,215
Other finfish	—	6,364
Other shellfish	391	1,411
Total	92,141	243,675

Reference: Rhodes 1988.

TABLE 6

World Aquaculture Production in 1975, 1980, and 1985, by Species Group (Thousands of Metric Tons)

Species group	1975	1980	1985
Finfishes	2628.8	3206.8	5697.2
Crustaceans	29.7	75.0	281.6
Mollusks	1961.2	3299.7	2885.7
Subtotal	4619.7	6581.5	8864.5
Seaweeds & other	NA	NA	3565.1
Total	NA	NA	12429.6

Reference: Rhodes 1989.

Alternative Uses for Fish Oil

The National Fish Meal and Oil Association submitted a petition to the U.S. Food and Drug Administration in 1986 requesting approval to use hydrogenated and refined fish oils in products for human consumption. The FDA recently granted approval for the hydrogenated oil, paving the way for its use in products such as shortenings and pastries. However, because of U.S. Department of Agriculture standards for margarine, fish oil still cannot be used in margarines.

The portion of the petition pertaining to refined fish oil is still pending. Unlike hydrogenated oil, refined oil contains omega-3 fatty acids, which have been shown to provide a wide variety of health benefits (Pique 1986). Adding refined fish oil to products such as salad dressings could enhance their nutritional value and marketability. However, the long-term prospects for this are uncertain, since (1) FDA approval may or may not be forthcoming, and (2) the technology necessary to address the problem of rancidity in refined oil is not well developed (Paul Bauersfeld, NMFS, Charleston, S.C., pers. comm.).

Japanese and South American Sardine Fisheries

Japan has historically been a major world producer of fish meal. From 1960 through 1971 Japan produced 9%–15% of the world's fish meal; its share of production increased to 15%–21% from 1972 through 1987. Until the mid-1980s Japan was also a net importer of meal (table 7).

Japan derives most of its fish meal from its sardine *(Sardinops melanosticta)* fishery, which has produced two periods of high yield in this century. Japan's sardine landings increased through the early 1900s to a peak of 1.75 million MT in 1935, then gradually declined to 9,200 MT by 1965 (Lluch-Belda et al., in press). Since 1965, landings have again increased dramatically (figure 5). Although Japan continues to take most of the harvest, the Soviet Union and South Korea have also participated in the fishery since the late 1970s.

TABLE 7

World Production and Japanese Production, Imports, and Exports of Meals and Solubles from Animals of Aquatic Origin (Thousands of Metric Tons)

Year	World production	Japan Production	Japan Imports	Japan Exports
1960	2,076.0	312.7	19.4	6.3
1961	2,580.0	362.2	23.3	4.9
1962	2,900.0	390.0	38.5	18.1
1963	2,902.0	328.4	84.3	3.6
1964	3,666.0	353.1	102.3	6.2
1965	3,615.0	344.5	112.6	13.1
1966	4,170.0	423.5	95.6	15.8
1967	4,660.0	420.3	86.8	11.3
1968	5,060.0	500.5	150.2	6.8
1969	4,750.0	594.2	108.0	183.0
1970	5,450.0	671.0	94.7	24.5
1971	5,400.0	692.0	21.7	37.7
1972	4,320.0	735.9	56.8	28.6
1973	4,020.0	791.0	87.3	17.8
1974	4,570.0	773.7	74.5	31.3
1975	4,510.0	839.6	70.6	49.3
1976	4,890.0	745.9	59.5	49.0
1977	4,575.4	857.2	181.1	37.5
1978	4,916.1	890.2	84.9	64.3
1979	5,089.9	895.6	101.6	57.7
1980	4,971.9	879.9	141.0	43.3
1981	5,056.2	898.9	84.1	73.7
1982	5,394.1	1,004.1	44.3	135.7
1983	5,282.6	1,133.5	95.1	79.6
1984	6,097.7	1,262.7	61.6	135.3
1985	6,275.2	1,166.6	80.3	157.4
1986	6,661.3	1,179.1	161.5	167.2
1987	6,394.6	1,112.7	187.3	216.6

Reference: Food and Agriculture Organization 1960–1987.

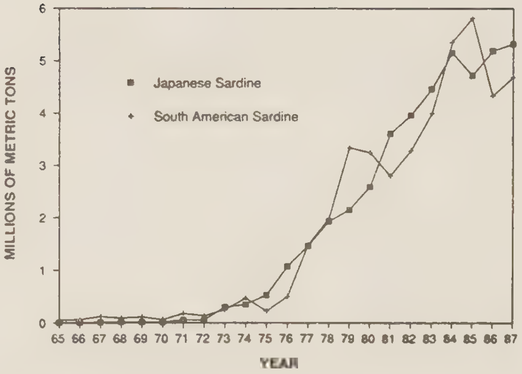

Figure 5. Landings of Japanese and South American sardine, 1965–87.

The South American sardine *(Sardinops sagax)* fishery has experienced similar rapid growth in the past two decades. Annual sardine landings by Chile and Peru have increased from negligible amounts in the mid-1960s to approximately 5 million MT (figure 5).

Given the record harvests experienced in recent years, the sardine fisheries of Japan and South America warrant close attention. A change in the status of these stocks could significantly affect the availability and price of fish meal.

New Products from Reduction Species

Efforts are ongoing to develop marketable products for direct human consumption from species traditionally used for reduction. For instance, a processor in Virginia has been exploring the economic feasibility of making a marketable surimi from menhaden (Malcolm Hale, NMFS, Charleston, S.C., pers. comm.). The Fishermen's Cooperative in San Pedro, California, is test-marketing canned sardines for human consumption. Although the ultimate outcome of these enterprises is uncertain, the expectation is that alternative uses will be found for reduction species over the long term.

Americanization of the Alaska Pollock Fishery

Significant increases in U.S. harvesting of and processing capacity for the Alaska pollock *(Theragra chalcogramma)* have resulted in a drastic curtailment of foreign landings and joint venture operations in recent years. As indicated in table 8, landings of Alaska pollock by foreign vessels declined from an

TABLE 8
Landings of Alaska Pollock (Metric Tons)

Year	Domestic	Joint venture	Foreign	Total
1977	323	0	1,009,826	1,010,149
1978	1,765	0	1,074,077	1,075,842
1979	2,551	0	1,047,150	1,049,701
1980	1,409	11,800	1,119,126	1,132,335
1981	1,741	58,950	1,117,455	1,178,146
1982	1,479	128,886	1,051,949	1,182,314
1983	1,382	283,104	973,050	1,257,536
1984	10,894	444,256	1,032,249	1,487,399
1985	42,109	614,337	851,870	1,508,316
1986	59,160	904,111	352,682	1,315,953
1987	250,407	1,057,315	3,596	1,311,318
1988	570,285	826,564	0	1,396,849

Reference: U.S. Department of Commerce 1977–1988.

approximate annual average of one million MT during 1977–85 to zero in 1988. Joint venture landings, which peaked at one million MT in 1987, are also expected to decline to zero in 1990, and domestic landings are expected to increase commensurately.

With the Americanization of the fishery and recent increases in fish meal processing capacity in shoreside plants and aboard U.S. factory trawlers, pollock meal is expected to become an increasingly large component of U.S. fish meal production. Additional impetus may be provided by the North Pacific Fishery Management Council, which is currently considering a change in regulations to require full use of the resource. Should such an amendment be adopted, it could lead to similar requirements for other Alaska groundfish species.

In 1988, the United States produced approximately 15,000 MT of pollock meal from the offal generated in the preparation of surimi and fillets/blocks (Vondruska et al. 1989). Assuming a fish meal yield of 10% from round weight (Steve Koplin, NMFS, Washington, D.C., pers. comm.) and an average annual harvest of 1.2 million MT, U.S. pollock meal production could reach 120,000 MT annually. This would be a significant addition to the 200,000 to 350,000 MT of fish meal that we currently produce each year.

Much of the pollock meal produced in recent years has been exported to Taiwan's eel farms (Jerry Babbitt, NMFS, Kodiak, Alaska, pers. comm.). Future increases in pollock meal production may also be exported abroad rather than absorbed into the U.S. market. Depending on the magnitude of this trade, the United States could reverse its long-standing status as a net importer of fish meal and become a net exporter.

LITERATURE CITED

FAO (Food and Agriculture Organization of the United Nations). 1960–1987. Yearbook of fishery statistics: fishery commodities.

———. 1986. The production of fish meal and oil. FAO Fisheries Technical Paper 142, 63 pp.

———. 1989. GLOBEFISH Highlights, no. 1/89:28.

Glantz, M.H. 1979. Science, politics and economics of the Peruvian anchoveta fishery. Mar. Policy 3(1):201–210.

Hansen, T. 1981/1982. A model of the world fish meal market. Fish. Res. 1:271–288.

Huppert, D. D. 1980. An analysis of the United States demand for fish meal. Fish. Bull. 78(2):267–276.

Kolhonen, J. 1974. Fish meal: international market situation and future. Mar. Fish. Rev. 36(3):36–40.

Lasker, R., and P. Smith. 1977. Estimation of the effects of environmental variation on the eggs and larvae of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19:128–137.

Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. In press. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci.

Pique, G. G. 1986. Omega-3: the fish oil factors. San Diego: Omega-3 Project, Inc., 163 pp.

Radovich, J. 1981. The collapse of the California sardine fishery: what have we learned? *In* Resource management and environmental uncertainty, M. H. Glantz, ed. New York: John Wiley & Sons, pp. 107–136.

Rhodes, R. J. 1988. Status of world aquaculture: 1987. Aquaculture magazine buyer's guide, pp. 4–18.

———. 1989. Status of world aquaculture: 1988. Aquaculture magazine buyer's guide, pp. 6–20.

Rogers, G. B. 1978. Costs, prices and productivity in the poultry and egg industries. Poultry and egg situation. Washington, D.C., U.S. Dept. of Agriculture, pp. 26–29.

Thomson, C. J. 1984. A model of fish meal supply and demand in the United States, 1966–1981. NMFS, SWFC Admin. Rep. LJ-84-04, 27 pp.

Thomson, C., C. Cooney, and J. Morgan. 1989. Status of the California coastal pelagic fisheries in 1988. NMFS, SWFC Admin. Rep. LJ-89-14, 23 pp.

Titus, H. W., and J. C. Fritz. 1971. The scientific feeding of chickens. Fifth edition. Danville, Ill. The Interstate Printers & Publishers Inc. 312 pp.

U.S. Department of Agriculture. 1960–1988. Agricultural statistics. Washington, D.C.

U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. 1971–1988. Fisheries of the United States. Washington, D.C.

U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries. 1960–1970. Fishery statistics of the United States. Washington, D.C.

Vondruska, J. 1980. Postwar production, consumption, and prices of fish meal. *In* Resource management and environmental uncertainty. M. H. Glantz, ed. New York: John Wiley & Sons, pp. 285–316.

Vondruska, J., R. Kinoshita, and M. Milazzo. 1989. Situation and outlook for surimi and surimi-based food. NOAA Technical Memorandum NMFS-SEFC-233, 16 pp.

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Age Estimation and Composition of Pelagic Armorhead *Pseudopentaceros wheeleri* from the Hancock Seamounts

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The pelagic armorhead *Pseudopentaceros wheeleri* is widely distributed in the North Pacific, but rarely collected until fishermen from the Soviet Union discovered large concentrations on the central North Pacific seamounts in the late 1960s (Sakiura 1972). The Soviet Union started a trawl fishery at the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts (29°N, 179°E to 35°N, 171°E) in 1967, and the Japanese entered the fishery in 1969 (Sasaki 1986). Since then, intensive fishing occurred at the Northwest and Southeast Hancock Seamounts, the southeast limit of the pelagic armorhead seamounts. During the 1970s, the pelagic armorhead catch rate by Japanese fishing vessels at the Hancock Seamounts declined dramatically (Uchida and Tagami 1984). Commercial fishing at the Hancock Seamounts ceased in 1984, and finally, a 6-year fishing moratorium went into effect in August 1986 (NMFS 1986).

Pelagic armorhead have an unusual life history. At SE–NHR seamounts, adults spawn during December–March, as indicated by ovarian studies (Sasaki 1974, Bilim et al. 1978) and the occurrence of larvae and young juveniles in February and March (Borets 1980). As juveniles, they apparently are pelagic and occur to the north and northeast of the seamounts as far as the Alaskan gyre before returning to the seamounts (Fujii 1986, Boehlert and Sasaki 1988). At the SE–NHR seamounts, most of the pelagic armorhead caught in the fishery are 26–33 cm fork length (FL), although 15–40 cm FL specimens occur (Humphreys and Tagami 1986). Larger specimens (>40 cm FL), but none 26–33 cm FL, have been caught on the northern Hawaiian Ridge, from Kure Atoll to French Frigate Shoals (Tagami and Humphreys, in prep.).

Pelagic armorhead at the seamounts exhibit three morphological types: fat, intermediate, and lean (Humphreys et al. 1984, 1989; Humphreys and Tagami 1986). During their pelagic phase and when they recruit to seamounts, they are "fat" and their gonads are in an early stage of development. When gonads begin developing and spawning occurs, they transform from an "intermediate" to a "lean" stage. It has not been determined whether the lean fish recover to spawn again.

In this study, we determined which hard part is the most suitable for estimating armorhead age and determined the temporal meaning of perceived daily growth increments and apparent annual check marks on the sagitta, the preferred hard part. Chikuni (1970) and Vasil'kov and Borets (1975) used annuli on scales to estimate age, but their estimates did not agree. Furthermore, neither study used validation procedures, nor did they document the area of collection. The criteria we developed were used to estimate the age composition of pelagic armorhead captured on Southeast Hancock Seamount.

Methods and materials

Specimen collection

Pelagic armorhead were obtained at the Hancock Seamounts in 1976–85 from the Japanese trawler *Kitakami Maru*, and by bottom trawl and handline from the NOAA ship *Townsend Cromwell*. Random samples were obtained by pooling specimens from bucket scoops (range 2–100 kg/haul) on the *Kitakami Maru*, during 1 August–15 October 1981, and from a single haul on the *Townsend Cromwell* on 24 July 1984. Fish were measured for FL to the nearest millimeter and sexed by gonadal examination. Fish were classified, on the basis of color and body depth, to one of three body types: fat, intermediate, or lean (Humphreys et al. 1984). We also included a few very large specimens caught by handline on the northern Hawaiian Ridge seamounts between Kure Atoll and French Frigate Shoals and postlarvae caught in a surface tow with a Tucker trawl at Southeast Hancock Seamount, 23–24 February 1985. All postlarval specimens were preserved and stored in 70% ethanol.

Hard-part selection and check-mark counts

To determine which hard part was most suitable for estimating age, 13 structures (Table 1) were dissected from 5 specimens collected at the Hancock Seamounts. The structures were prepared for examination following modified procedures of Six and Horton (1977). The hypural

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Table 1
Comparison of check marks on various hard parts of five *Pseudopentaceros wheeleri* from the Hancock Seamounts.

	No. check marks by fish identification number				
Hard part	343	350	338	385	383
Sagitta	3	3	—	3	2
Centrum (vertebra)	3	3	3	3	2
Dorsal spine	3	3	3	3	2
Dorsal ray	0	0	0	0	0
Anal spine	3	0	3	3	2
Anal ray	0	0	0	0	0
Pelvic spine	0	0	3	3	0
Pelvic ray	0	0	0	0	0
Pectoral spine	0	0	0	0	0
Pectoral ray	0	0	0	0	0
Hypural	3	3	3	3	2
Maxillary	0	0	3	3	2
Scales	0	—	—	—	0

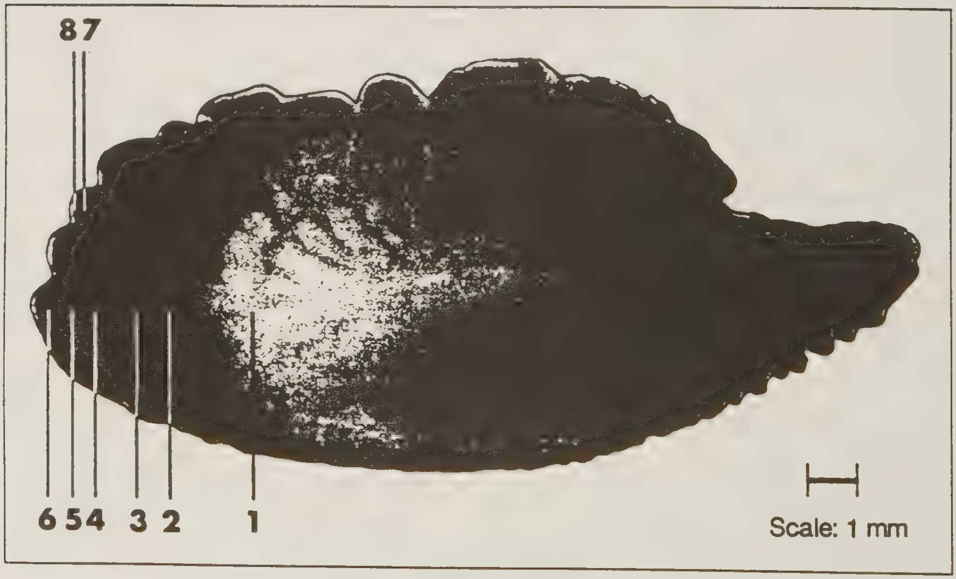

Figure 1
Sagitta of *Pseudopentaceros wheeleri* with annuli marked and numbered.

plate, maxillary, and vertebrae were cleaned of tissue and dried. Spines and rays of the dorsal, pelvic, pectoral, and anal fins were cleaned of tissue, embedded in resin, cross-sectioned in a continuous series from the base, and examined under a compound microscope. Both surfaces of a section were examined. Tissues were also examined under a dissecting microscope with reflected and transmitted light.

Sagittae were sanded lightly on the surfaces with no. 400 grit carborundum sandpaper, then, with a dissecting microscope, were examined whole against a black background while submerged in water. Check marks appeared as pairs of bright (opaque) and dark (translucent) concentric bands under reflected light (Fig. 1).

Scales were taken from nine different areas of the body. Three sites were along the lateral line: below the first dorsal spine, midway along the lateral line, and below the posterior end of the dorsal fin. Three sites were midway between the lateral line sites and the dorsal fin, and three were midway between the lateral line sites and the ventral border. Scales were taken from 20 fish of three different body types and from 13 fish, caught in February 1985, with three check marks on their sagittae. After being cleaned, scales were mounted in Euparal under a cover glass on a glass slide or flattened between two glass slides after being air dried.

Selection of the hard part for ageing was based on the consistency of perceived annual check mark counts and ease of preparation (Table 1). Only the sagittae, vertebral centrum, hypural plate, and dorsal and anal fin spines showed check marks. Counts of check marks from each part were identical (Table 1), indicating these structures could be used for estimating age if their check marks could be verified as annuli. The number of check marks on vertebral centrum, hypural plate, and maxillary was reduced by half upon drying. Soft rays of dorsal, pelvic, pectoral, and anal fins showed no marks that could be interpreted as check marks. Scales were without check marks, and their circuli appeared evenly spaced. Of all the structures compared, the sagitta was considered the best structure for estimating the age of pelagic armorhead.

Counts of daily growth increments

Sagittae removed at sea were stored in fresh water in vials and refrigerated; those not extracted at sea were frozen within the head and later removed in the laboratory. Sagittae were sanded lightly on both sides with no. 400 carborundum sandpaper until translucent and etched in a very dilute solution of HCl for 3–5 minutes. The acid was diluted until only 1–2 bubbles per second were formed in reaction to the calcium carbonate of the sagitta. This process was repeated until the increments became visible from the core to the tip of the postrostrum. The sagittae of postlarval specimens were teased from the skull, cleaned, and mounted in Euparal without further processing. To support the coverslip, each sagitta was mounted on a microscope slide in Euparal by using short segments of monofilament line slightly greater in diameter than the thickness of the otolith. Sagittae were examined under a compound microscope at 300× magnification.

Increment counts often took a circuitous route between the core and the tip of the postrostrum; the mean of 10 counts was used as the age estimate. Increment counts were routine for sagittae with two check marks but were more difficult for those with three check marks. Increment width in translucent zones decreased with increasing number of check marks (8.3 μm during year 1, 1.7 μm during year 2, and 1.5 μm during year 3), and incremental pattern was more variable after year 2.

Age estimation

Check marks could not be validated as annuli by conventional means (Beamish and McFarlane 1983). Mean increment counts were used to estimate the hatching time, assuming the first increment formed at or soon after hatching. This technique, though low in accuracy, may suffice when direct validation is unattainable (Gjøsaeter et al. 1984). To verify check marks as annuli, mean counts of growth increments for fish caught in February were then compared with counts of check marks, which were multiplied by 365.

Age composition of catches of pelagic armorhead at Southeast Hancock Seamount was based on check-mark counts (i.e., perceived annuli). Mean FLs between age-sex groups were compared using the Mann-Whitney paired test, since unequal variances occurred in one sample. To increase sample size of age-sex groups from the *Kitakami Maru* catch, randomly sampled specimens from Northwest and Southeast Hancock Seamounts were combined.

Results and discussion

Increment counts from demersal and oceanic adults and juvenile pelagic armorhead suggested that increments were deposited daily (Tables 2 and 3). A total of 88% of the estimated hatching dates of adults occurred within the spawning period, and the other three hatching dates were reasonably close to the spawning period.

Check marks appeared to be valid annuli based on number of daily growth increments for fish caught in February (Table 2). Sagittae with two check marks had approximately 730 increments (range 728–773, $N=5$), and those with three check marks had about 1095 increments (range 1037–1128, $N=4$). Check marks were also verified as annuli by a second but less precise method (Pannella 1971). Partial counts of 365 apparent daily growth increments appeared to coincide closely with the first pair of opaque and translucent zones of sagittae of age-1 and -2 fish. Partial counts of about 730 apparent daily growth increments corresponded with the outer margin of the second translucent zone on sagittae of age-2 fish.

Fish caught in summer appeared to have completed check marks on their sagittae. Sagittae from fish caught in July with two check marks had increment

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Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 2

Age estimates of pelagic armorhead *Pseudopentaceros wheeleri* by counting apparent daily growth increments (GI) on sagittae.

Date captured	Fork length (mm)	Sex	Mean GI count	SD	Estimated hatching date	No. check marks	Body type
29 Oct. 1976	277[a]	M	623	25.63	8 Feb. 1975	2	—
18 June 1983	340	F	902	13.04	29 Dec. 1980	3	Fat
12 July 1984	300	F	576	24.03	13 Dec. 1982	2	Lean
12 July 1984	322	F	621	21.67	30 Oct. 1982	2	Intermediate
13 July 1984	305	M	549	43.83	10 Jan. 1983	2	Intermediate
13 July 1984	308	F	937	58.00	18 Dec. 1981	3	Lean
24 July 1984	309	M	907	94.29	28 Jan. 1982	3	Fat
24 July 1984	310	M	544	37.28	26 Jan. 1983	2	Fat
24 July 1984	322	M	923	92.46	13 Jan. 1982	3	Fat
24 July 1984	329	F	605	37.94	26 Nov. 1982	2	Fat
25 July 1984	307	F	586	37.16	16 Dec. 1983	2	Intermediate
25 July 1984	319	F	914	39.99	22 Jan. 1982	3	Intermediate
29 July 1984	303	M	853	51.39	28 Mar. 1982	3	Intermediate
16 Feb. 1985	282	M	728	46.10	18 Feb. 1983	2	Lean
16 Feb. 1985	290	M	1037	26.80	15 Apr. 1982	3	Lean
16 Feb. 1985	293	M	762	50.96	15 Jan. 1983	2	Fat
16 Feb. 1985	304	F	758	40.53	19 Jan. 1983	2	Lean
16 Feb. 1985	311	F	761	45.73	16 Jan. 1983	2	Lean
16 Feb. 1985	317	M	773	27.29	4 Jan. 1983	2	Lean
16 Feb. 1985	319	F	1128	79.66	14 Jan. 1982	3	Lean
16 Feb. 1985	320	F	1101	84.65	10 Feb. 1982	3	Lean
23 Feb. 1985	355	F	1065	51.32	25 Mar. 1982	3	Fat
25 July 1984	322[b]	M	951	69.04	16 Dec. 1981	3	Fat
25 July 1984	305[c]	—[d]	599	35.83	3 Dec. 1982	2	Fat
25 July 1984	310[e]	F	580	52.73	22 Dec. 1982	2	Fat

[a] Estimated from standard length.

[b] *Oshoru Maru*, lat. 45°26′N, long. 154°58′W.

[c] *Oshoru Maru*, lat. 45°26′N, long. 155°00′W.

[d] Gonad undeveloped.

[e] *Oshoru Maru*, lat. 45°26′N, long. 155°00′W.

Table 3

Age estimates of postlarval *Pseudopentaceros wheeleri*, determined by counts of apparent daily growth increments (GI) on sagittae.

Fork length (mm)	Capture date	Mean GI count	SD	Estimated hatching date
12.1	24 Feb. 1985	36.5	1.72	19 Jan. 1985
12.1	24 Feb. 1985	34.7	1.89	20 Jan. 1985
13.4	24 Feb. 1985	39.6	2.41	15 Jan. 1985
13.6	23 Feb. 1985	42.1	2.02	12 Jan. 1985
13.6	24 Feb. 1985	41.9	2.64	12 Jan. 1985
15.9	23 Feb. 1985	41.9	2.28	12 Jan. 1985
15.9	23 Feb. 1985	48.0	5.16	6 Jan. 1985
18.2	23 Feb. 1985	57.7	5.93	27 Dec. 1984

counts (544–621) roughly equivalent to 1.5 years, and those with three check marks had increment counts (853–937) roughly equivalent to 2.5 years (Table 2). In July, sagittae of age-1 and -2 fish appeared to have two and three translucent zones, respectively. The outer translucent zone probably was due to thinness at the edge of the sagittae. Another possibility is that the opaque zone formed over a short period (<2 months) and formed internally in the translucent zone so that the outer edge was opaque for only a brief period. This has also been observed for *Ammodytes tobianus* (Reay 1972). Regardless, the result would be an overestimation of age for part of the year if fish were sampled prior to the spawning season.

Table 4

Mean fork lengths (FL) of pelagic armorhead *Pseudopentaceros wheeleri* age groups at the Southeast Hancock Seamount.

		Male FL (mm)				Female FL (mm)			
Sample date	Age	Range	Mean	SD	*N*	Range	Mean	SD	*N*
Aug.–Oct. 1981	1.5	267–320	294	14.07	37	285–325	307	9.54	68
	2.5	304–304	304		2	283–329	310	14.08	8
July 1984	1.5	247–330	301	15.57	37	295–331	308	8.22	39
	2.5	285–326	307	13.96	13	290–342	315	10.89	27

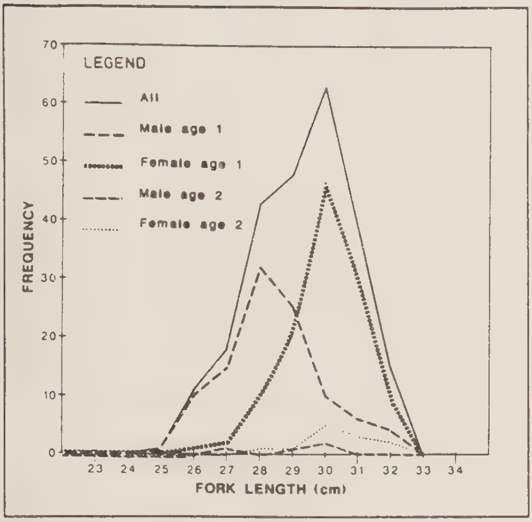

Figure 2

Length-frequency distribution of *Pseudopentaceros wheeleri* sampled at the Hancock Seamounts, 1 August–15 October 1981.

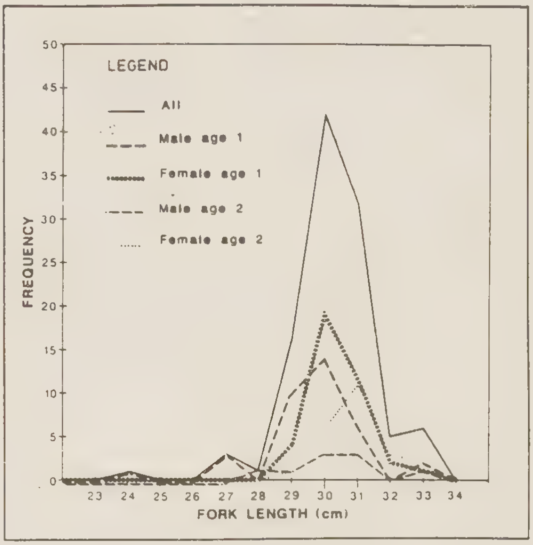

Figure 3

Length-frequency distribution of *Pseudopentaceros wheeleri* sampled at the Southeast Hancock Seamount, 24 July 1984.

We could not determine when the opaque zone formed because specimens were not obtainable throughout the year and the edge always appeared translucent.

Pelagic armorhead from the summer trawl fishery at the Southeast Hancock Seamount consisted of fish approximately ages 1.5 and 2.5, and yearlings were dominant in both 1981 (96%) and 1984 (66%) (Table 4). Yearling females appeared to be larger than males in both 1981 and 1984 samples (Figs. 2 and 3; Table 4). Differences between male and female mean lengths were significant in 1981 ($P<0.001$) and in 1984 ($P=0.025$), but difference in mean lengths for year-2 females and males in 1984 was not significant ($P=0.107$). The latter could have been due to small sample size; hence, larger samples should be examined before requiring separate growth curves for males and females. Our samples were not perfectly suited for group comparison because sex and age were unknown when the random samples were taken. Thus, unequal group size and unequal variances occurred. Due to our small sample size, slight skewness and kurtosis were encountered in comparing central tendencies of some age-sex groups. However, only the unequal variance between groups was serious enough to have affected the analyses.

Pelagic armorhead may attain sexual maturity before they reach the seamount. We base this on the age-length relationships of the three oceanic specimens (Table 2). After pelagic armorhead settle on the seamount, it appears that little growth occurs. Length-frequency distribution reported by other investigators (Sasaki 1986, Wetherall and Yong 1986) tends to confirm this observation. The lack of older (>age 3) individuals on the seamounts suggests that pelagic armorhead may spawn only one or two seasons and then die. Indeed, the presence of emaciated individuals suggests some postspawning mortality (Humphreys et al. 1984, Humphreys and Tagami 1986). Conversely, the existence of larger and older specimens in the northwestern Hawaiian Islands would suggest that longer life is possible and different life histories occur in different environments. Of the sagittae from large pelagic armorhead examined for comparison purposes, fish 43–48 cm FL ($N = 3$) had four check marks, fish 48–54 cm FL ($N = 2$) had five check marks, and the largest fish, 54.7 cm FL, had eight-plus check marks (Fig. 1). Although the relationship of these large pelagic armorhead to those on the seamounts is unknown, it is plausible that during the pelagic stage juveniles were displaced to the east, entered the subtropical gyre, and grew larger while spending 1–3 years longer in the open ocean before settling in the northern Hawaiian Ridge seamounts, southeast of the SE-NHR seamounts (Boehlert and Sasaki 1988).

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Citations

Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.

Bilim, L.A., L.A. Borets, and L.K. Platoshina
1978 Characteristic of ovogenesis and spawning of the boarfish in the region of the Hawaiian Islands. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khloz. Okeanogr. (TINRO) 102: 51–57 [In Russ., Engl. abstr.] (Engl. transl. by W.G. Van Campen, 1986, Transl. 106, 9 p.; avail. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

Boehlert, G.W., and T. Sasaki
1988 Pelagic biogeography of the armorhead, *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. Fish. Bull., U.S. 86:453–465.

Borets, L.A.
1980 The distribution and structure of the range of the boarfish *Pentaceros richardsoni*. J. Ichthyol. 20(3):141–143.

Chikuni, S.
1970 The "phantom fish," "Kusakari tsubodai"—An outline. Enyo (Far Seas) Fish. Res. Lab. News 3:1–4, Feb. 1970. (Engl. transl. by J.H. Shohara, Natl. Mar. Fish. Serv., NOAA, Terminal Island, CA 90731.)

Fujii, E.
1986 Zoogeographical features of fishes in the vicinity of seamounts. *In* Uchida, R.N., S. Hayasi, and G.W. Boehlert (eds.), Environment and resources of seamounts in the North Pacific, p. 67–69. NOAA Tech. Rep. NMFS 43, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

Gjøsaeter, J., P. Dayaratne, O.A. Bergstad, H. Gjøsaeter, M.I. Sousa, and I.M. Beck
1984 Aging tropical fish by growth rings in the otoliths. FAO Fish. Circ. 776, 54 p.

Humphreys, R.L., Jr., and D.T. Tagami
1986 Review and current status of research on the biology and ecology of pelagic armorhead. *In* Uchida, R.N., S. Hayasi, and G.W. Boehlert (eds.), Environment and resources of seamounts in the North Pacific, p. 55–62. NOAA Tech. Rep. NMFS 43, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

Humphreys, R.L., Jr., D.T. Tagami, and M.P. Seki
1984 Seamount fishery resources within the southern Emperor-northern Hawaiian Ridge area. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proceedings of the second symposium on resource investigations in the northwestern Hawaiian Islands, May 25–27, 1983, vol. 1, p. 283–327. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii, Honolulu.

Humphreys, R.L., Jr., G.A. Winans, and D.T. Tagami
1989 Conspecific status of the North Pacific species of pelagic armorhead, *Pseudopentaceros wheeleri* and *P. pectoralis*. Copeia 1:142–153.

NMFS (National Marine Fisheries Service)
1986 Western Pacific bottomfish and seamount groundfish fisheries. Rules and Regulations, 50 CFR Part 683. Federal Register 51(147):27413-27419.

Pannella, G.
1971 Fish otoliths: Daily growth layers and periodical patterns. Science (Wash., DC) 173:1124–1127.

Reay, P.J.
1972 The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus* L. J. Cons. Cons. Int. Explor. Mer 34(3):485–504.

Sakiura, H. (translator)
1972 The pelagic armorhead, *Pentaceros richardsoni*, fishing grounds off the Hawaiian Islands, as viewed by the Soviets. Suisan Shuho 658:28–31. (Engl. transl. by T. Otsu, 1977, Transl. 17, 7 p.; avail. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

Sasaki, T.
1974 The pelagic armorhead, *Pentaceros richardsoni* Smith, in the North Pacific. Bull. Jpn. Soc. Fish Oceanogr. 24:156–165. (Engl. transl. by T. Otsu, 1977, Transl. 16, 13 p.; avail. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
1986 Development and present status of Japanese trawl fisheries in the vicinity of seamounts. *In* Uchida, R.N., S. Hayasi, and G.W. Boehlert (eds.), Environment and resources of seamounts in the North Pacific, p. 21–30. NOAA Tech. Rep. NMFS 43, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

Six, L.D., and H.F. Horton
1977 Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405–414.

Tagami, D.T., and R.L. Humphreys, Jr.
In prep. Occurrence of pelagic armorhead, *Pseudopentaceros wheeleri*, in the northwestern Hawaiian Islands waters. Honolulu Lab. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

Uchida, R.N., and D.T. Tagami
1984 Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46(2): 1–17.

Vasil'kov, V.P., and L.A. Borets
1975 Determining the age of boarfishes by spectrophotometric analysis of scale structure. Soviet J. Mar. Biol. (Engl. transl. Biol. Morya) 4(1):545–548.

Wetherall, J.A., and M.Y.Y. Yong
1986 Problems in assessing the pelagic armorhead stock on the central North Pacific seamounts. *In* Uchida, R.N., S. Hayasi, and G.W. Boehlert (eds.), Environment and resources of seamounts in the North Pacific, p. 73–85. NOAA Tech. Rep. NMFS 43, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv.

9066

USING MESH SIZES TO REDUCE DISCARDS

EDWARD UEBER, Gulf of the Farallons Marine Sanctuary

Mesh selectivity can result in a greater degree of fish selectivity than can generally be obtained with other fishing gear. Generally, mesh selectivity is more effective if the net is stationary. When a net is moving through the water, the mesh can fill, and this condition can cause the net to lose its selectivity. However, when the bag of a trawl net fills, catchability of the net decreases because of the pressure at the net mouth. Net design can change the selectivity of a given mesh size.

Mesh selectivity is greatest in single-species fisheries such as Pacific herring. Effective regulation of fish size decreases as the number of species within a fishery increases. For example, flatfish will go through the mesh differently than lingcod (*Ophiodon elongatus*) or rockfish. An effective net for a flatfish may be ineffective for a round fish, resulting in a catch of round fish that may be too young for breeding or too small to be sold. You must be very careful when you design your mesh size that you know what the net's effect will be on the long-term productivity of a fishery.

One associated discard problem is the simultaneous catch of marketable and nonmarketable sizes of the same species. Increasing the size of the mesh may enable smaller fish to escape to be caught later when they are bigger and more marketable.

Mesh sizes on the West Coast have also been implemented to stop the gilling problem. Some people don't perceive gilling as a problem, but fish do get gilled in the meshes and must be extracted. An instance where gilling caused a major problem occurred in the Pacific sardine fishery when a net would "Christmas tree" with small sardines, and almost every mesh would contain a sardine. I have spoken with a fisherman out of Coos Bay who uses five-inch mesh to fish for widow rockfish (*Sebastes entomelas*). He said he had a gilling problem, but all of the fish gilled were saleable. If he had used a smaller mesh net, he would have had to remove and discard the smaller fish because they would have been too small to sell.

Sometimes mesh is used in gillnet fisheries to select a certain species or certain size of fish. In San Francisco Bay, the California Department of Fish and Game has increased the mesh size for gillnets used to fish for herring. The larger mesh nets, when fished over a given time period, increase the size of herring being caught. Larger herring tend to be female and this results in the overall herring catch having a greater roe female and this results in the overall herring catch having a greater roe content and greater value. In this roe fishery worth $20 million, almost all male fish caught are discarded. Fishermen do not discard them at sea because it is difficult to separate the males from the females there. As much as 50 percent of the catch may not have roe and be discarded by the processor.

9067

2. THE COLLAPSE OF CALIFORNIA'S SARDINE FISHERY (Ueber & MacCall)

The California sardine fishery has become legendary in American folklore. The fishery began before the turn of the last century, peaked in the 1930s and began to collapse after World War II. It is a classic case of the rise and fall of a fishery dependent on a pelagic species, of overcapitalization of an industry, and of too many fishing boats using new technologies to harvest a fragile, if not dwindling, resource. Its collapse spawned the rapid development of similar fisheries in Peru, Chile and South Africa, each of which then underwent essentially the same kind of growth and decline as the California sardine fishery. This fishery can be used as an analogy of potential changes that might accompany the regional consequences of a global warming of the atmosphere and could provide lessons for proactive as well as reactive responses to changes in abundance of a pelagic industrial fishery.

The canning of sardines (*Sardinops sagax*) along the California coast began in the late 1800s, and with intermittent successes and failures became the largest fishery on the West Coast by 1925. By then sardine catches were being used for reduction to fish meal as well as for food. The industry landed 173,000 tons of sardines off coastal California and an additional 1000 tons off the British Columbian coast in the 1925–26 season (Figure 6).

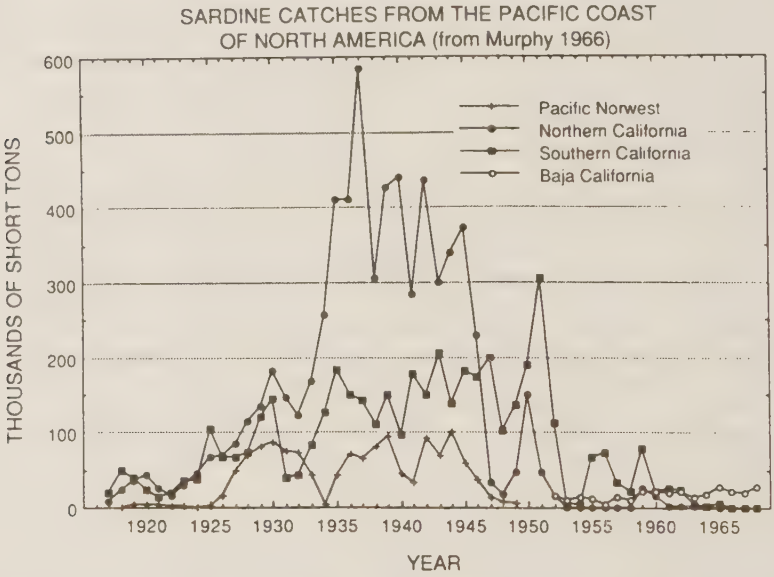

Figure 6. Sardine catches from the Pacific coast of North America. Pacific Northwest includes British Columbia, Washington, and Oregon. Northern California includes reduction ships, San Francisco, and Monterey (data from Murphy, 1966).

The sardine fishery began as a supplier of fresh whole fish in the 1860s; sardines had also been used as bait since the 1880s. The shift to the canning of sardines between the 1890s and 1920s actually created two new industries. The first of these produced a high quality, highly valued canned sardine for human consumption. The second produced a protein-rich feed for poultry as well as fertilizers for green plants. Poultry feed and plant fertilizer were produced from waste using a process called "reduction." The value of this canned sardine by-product soon caused canneries to set up their own reduction plants. By 1920, increased demand for sardine meal and fertilizer prompted some plants to use the whole fish as well as canning waste to produce fish meal, flour, oil and fertilizer.

The California Department of Fish and Game became concerned about the increases in direct use of sardine for non-human consumption. In every year between 1920 and 1941 (excluding only 1923 and 1924), new laws were passed to curtail the use of whole fish for reduction. The law stated that only those plants that canned fish for food could legally reduce sardines. As a result, canned sardines were produced and sold at or below cost so that canneries could obtain enough waste and whole fish for reduction.

The high quality of canned California sardine assured an increasing demand for the product in the marketplace. Canners also received another benefit from maintaining high quality; it enabled more by-product per ton of fish landed because there would be an increase in the amount of offal and unsuitable whole fish (the higher the canned quality).

Although state and federal governments were in agreement on the need to reserve the sardine resource for human consumption, the economics of reduction and the legal system dictated against conservation. A major loophole in the legal structure was uncovered that allowed for fish to be caught and processed outside the state's three-mile territorial jurisdiction. More specifically, the state's ability to assure that sardine be used for human consumption was challenged during the 1926-27 season, when a Monterey canner towed the concrete barge "Peralta" outside the state's three-mile jurisdiction in order to reduce whole sardine to fish meal. The economics of this operation failed but other similar ventures followed. In the early 1930s a few such ventures began to operate profitably. Floating reduction plants became a common sight off the major sardine ports from San Diego to San Francisco.

These vessels operated until the late 1930s (Figure 7), when prices for fish meal and fish oil fell and when an amendment to the California constitution was passed. This amendment provided California with the authority to stop the operations of offshore reduction plants. In the preceding nine seasons, which happened to have occurred during some of the most abundant years in the sardine fishery, reduction ships landed about 780,000 tons of sardine. At-sea sardine purchases made up about 16% of the sardine landings during this period.

Washington and Oregon entered the sardine fishery in the 1936-37 season and their landings, along with those of California and British Columbia, accounted for the largest one-season landings of any single fish species ever caught on the West Coast, more than 790,000 tons. As one author noted, this is enough ten-inch sardine, if laid end to end, to reach from the earth to the moon and back!

The twelve seasons from 1934 to 1946 could be considered the *pax sardinia* in the California fishing industry. World War II caused prices to rise for fish oil, meal, fertilizers and canned sardines. Landings averaged about 600,000 tons per season. However, State fishery biologists had been warning the industry that the sardine population could not sustain removals of more than 250,000 tons. Federal agencies as well as the industry opposed any such regulations in the

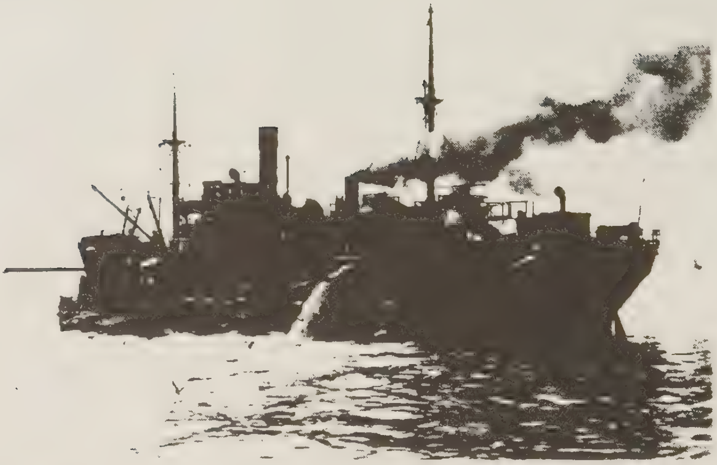

Figure 7. *Lake Miraflores*, the first reduction ship to operate outside the jurisdiction of the State of California, unloading sardines from a purse seiner in the early 1930s (Glantz and Thompson, 1981).

form of catch quotas. In his novel *Sweet Thursday*, John Steinbeck wrote that "The canneries themselves fought the war by getting the limit taken off fish and catching them all. It was done for patriotic reasons . . . ."

Between 1946 and 1952 annual landings averaged about 230,000 tons, about 40% of the previous 12-season average. During the next ten seasons (until 1962), recorded landings averaged 55,322 tons. The last six seasons produced a landings average of 24,000 tons. The fishery ended in 1968.

The search for causes for the demise of the California sardine fishery has focused at one time or another on overfishing, conflicting management schemes, climate variability or some combination of these. The loss of the sardine fishery had ramifications for the West Coast fishing community, the state of California and some Central American, South American and African nations.

The majority of canned sardines and fish meal production came from the Monterey and San Francisco areas, and from Southern California (Figure 8). The most famous of the sardine canning communities is Monterey, most likely because of the focus on the region in the writings of author John Steinbeck. It is important to note that Monterey products were considered top-of-the-line, also contributing to their recognition. Monterey did not suffer as much as most other areas in the US during the Great Depression, because sardine production remained high and even increased in the late 1930s. During the war years, fish oil was the big money-earner, not canning. Investing in reduction plants was a way for those involved in the fishery to prosper.

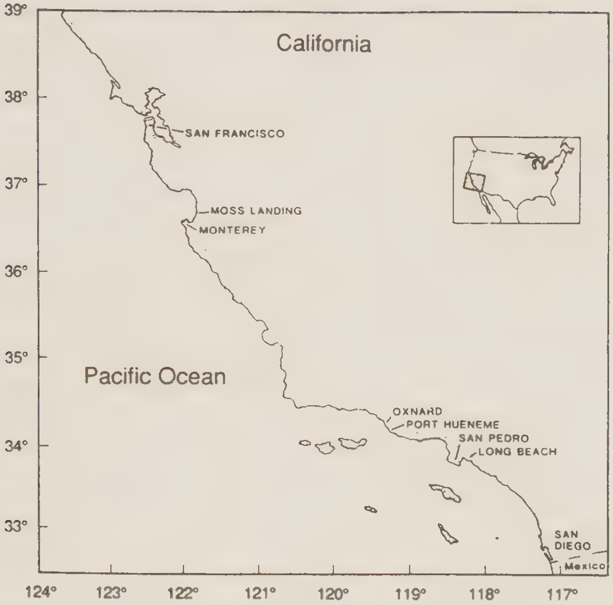

Figure 8. Location of California cities.

Although reduction plants had ceased to operate by 1950, Monterey canneries remained open until 1957. However, most of the fish canned there in the 1950s had to be trucked in from Southern California, with fishermen paying the shipping costs. By 1960 only the bait fishery remained in Monterey. In 1968 sportfishermen were paying one dollar per sardine. Sardine fishing ended in southern California that year. Thus, by 1968, the fishery was gone, eighty years after it had begun in San Francisco.

The collapse itself had occurred over twenty-two seasons. Fishermen had been witnessing declining catches for years with fewer and smaller schools of sardine appearing. Nevertheless, as late as the 1950s, fishermen spoke of the return of the sardine. With an occasional decent season, such as 1958/59 when 126,000 tons were landed, people kept hoping for the return for several more years.

A typical multi-fishery pattern consisted of fishing for salmon off the west coast of Alaska (June to September), sardine off the California coast (October to March) and squid near San Pedro and Monterey (April, May and sometimes September). Those who participated in this multi-fishery had some options. For example, smaller vessels fished market (Dungeness) crabs (*Cancer magister*) from November to February; others fished rockfish (*Sebastes spp.*), albacore tuna (*Thunnus alalunga*) and salmon (*Oncorhynchus spp.*). Shifts to other fisheries were often accompanied by crew reductions. Vessels that were unable to switch, for example, from lampara or seine gear fished for squid, anchovy or tuna. None of the displaced American fishermen or fish processing workers received assistance or were retrained by the US Government.

Those who could no longer pay the mortgage or upkeep on their vessels sold them, often at prices well below their original costs. Some of the larger vessels went to Alaska to participate in the expansion of the king crab (*Paralithodes camtschatica*) fishery. The low cost of these vessels kept fixed costs down, affording the new owners the luxury of learning to fish and market different products while having to cover little more than operating costs.

At the same time that vessels were being sold and transferred to other West-Coast fisheries, idled vessels and canning and processing equipment were sold in the international marketplace to such countries as Peru, Chile and South Africa. The UN FAO and the UNDP assisted with these purchases.

Fish meal and oil reduction machinery constituted the majority of equipment to South America. This equipment was generally older and less costly than comparable equipment sold to the South Africans. The transfer of and low costs for this equipment, as was the case in Alaska, allowed for a rapid expansion of the sardine and anchoveta (*Engraulis ringens*) fisheries off the west coast of South America.

Funds supplied by these UN agencies were also used to obtain expertise in canning, reduction, and fishery management. Fishing expertise was also transferred to these newly developed overseas fisheries. For example, lampara fishermen from San Francisco and seiners from San Diego went to South America for up to a year to teach fishing methods or to work as contract skippers. Some sold their vessels, delivered them in South America and stayed on as skippers.

Fisheries scientists as well as managers from California and elsewhere became involved in the management of South American fisheries as a result of UN support for the development of the well-respected Instituto del Mar del Peru (IMARPE). Many of these scientists had been involved in the assessment and management of the California sardine fishery. Like many of the industry's workers, these scientists had gone to South America "to search for new raw material" for their scientific skills.

Lessons

In response to global climate change some fisheries may decline or collapse, while others may increase and prosper. The history of the collapse of a major fishery like the California sardine fishery provides a number of lessons on how local, national and international fishing activities might be expected to respond to the regional implications of a global warming. These lessons clearly indicate the path that a newly developed clupeoid fishery may be expected to take and, more importantly, they indicate that strong management is needed to counter destructive tendencies. Lessons suggested by this fishery case study are as follows:

- Overfishing can cause fishery collapse rather than a sustained low-level harvest.
- Development-oriented government agencies can contribute toward delayed and ineffective fisheries management.
- Non-market funding of equipment or expertise will cause the fishery to develop more rapidly than would be expected from purely market-driven development (for example, the use of the US Navy and Coast Guard to locate schools of sardine).
- Fisheries management can behave like a subsidy because it encourages investment if its perceived presence engenders optimism or decreases the expectation of risk.
- A substitute fishery will develop more rapidly than a newly developed independent fishery, because existing capital, labor, technology and markets can readily be transferred to the substitute fishery.
- The instant availability of technology and expertise eliminates the "learning curve" and the rapid transfer of expertise, technology and processing capacity will exacerbate inherent instability in the fishery.
- The political process of establishing management institutions and the scientific process of developing predictive fishery models are much slower than the processes associated with industrial development of substitute fisheries.
- Internationally, governments and their fishery management agencies should be prepared to adopt politically difficult (and industry-resisted) management policies of deliberately constrained fishery development and should avoid politically popular but destabilizing subsidies.

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Hawaiian Monk Seal Pupping Locations in the Northwestern Hawaiian Islands[1]

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ABSTRACT: Most births of the endangered Hawaiian monk seal, *Monachus schauinslandi*, occur in specific beach areas in the Northwestern Hawaiian Islands. Data collected from 1981 to 1988 on the locations of monk seal births and of the first sightings of neonatal pups were summarized to identify preferred birth and nursery habitats. These areas are relatively short lengths of beach at the breeding islands and have some common characteristics, of which the primary feature is very shallow water adjacent to the shoreline. This feature, which limits access by large sharks to the water used by mother-pup pairs during the day, should enhance pup survival.

THE HAWAIIAN MONK SEAL, *Monachus schauinslandi*, is an endangered species that occurs primarily in the Northwestern Hawaiian Islands (NWHI) from Nihoa Island to Kure Atoll (Figure 1). The seals breed at these locations as well, with births mainly occurring from March through June and peaking in May. Sightings of monk seals are frequent around the main Hawaiian Islands and rare at Johnston Atoll, about 1300 km southwest of Honolulu (Schreiber and Kridler 1969). Recently, a tagged seal was observed near Wake Island, about 3650 km west of Honolulu (M. Pons, pers. comm.), and two monk seals were seen at Palmyra Island, 1670 km south of Honolulu (J. Hughes, pers. comm.).

In the late 1950s, about 1200 monk seals were counted on NWHI beaches, but by the mid-1970s, counts revealed less than half that number (Kenyon and Rice 1959, Johnson et al. 1982). Counts at some locations at the northwestern end of the Hawaiian Archipelago had declined by more than 90%, while the number of observed seals grew at least sixfold at French Frigate Shoals (FFS). These changes left very small breeding populations at Kure Atoll, Midway Islands, and Pearl and Hermes Reef. Some of the reduced counts were reportedly due to human disturbance (Kenyon 1972). Depleted also, but less dramatically during that time, were the populations at Lisianski and Laysan islands. Although one could speculate that a net eastward movement of seals could account for the increase in seals at FFS along with the reductions at the western end, the available data on resightings of tagged individuals do not support such a conclusion (Johnson and Kridler 1983).

During the last decade, monk seal births were confirmed at all of the NWHI: Nihoa Island, Necker Island, FFS, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Islands, and Kure Atoll (Figure 1). In the main Hawaiian Islands, a single birth occurred in 1988 on the island of Kauai, and there have been unconfirmed reports of a few births per year on Niihau. Some females show high fidelity for previous parturition sites. Mother-pup pairs generally stay near the birth site in the early weeks of nursing, but some may slowly move along the beach, up to a few hundred meters away from the birth site, as the pup gets older and weaning time approaches (Alcorn 1984). Weaning occurs at 5 to 6 weeks of age.

Birth and nursing sites around the breeding islands tend to be concentrated at specific beach locations, based on several years of observations during the prolonged pupping

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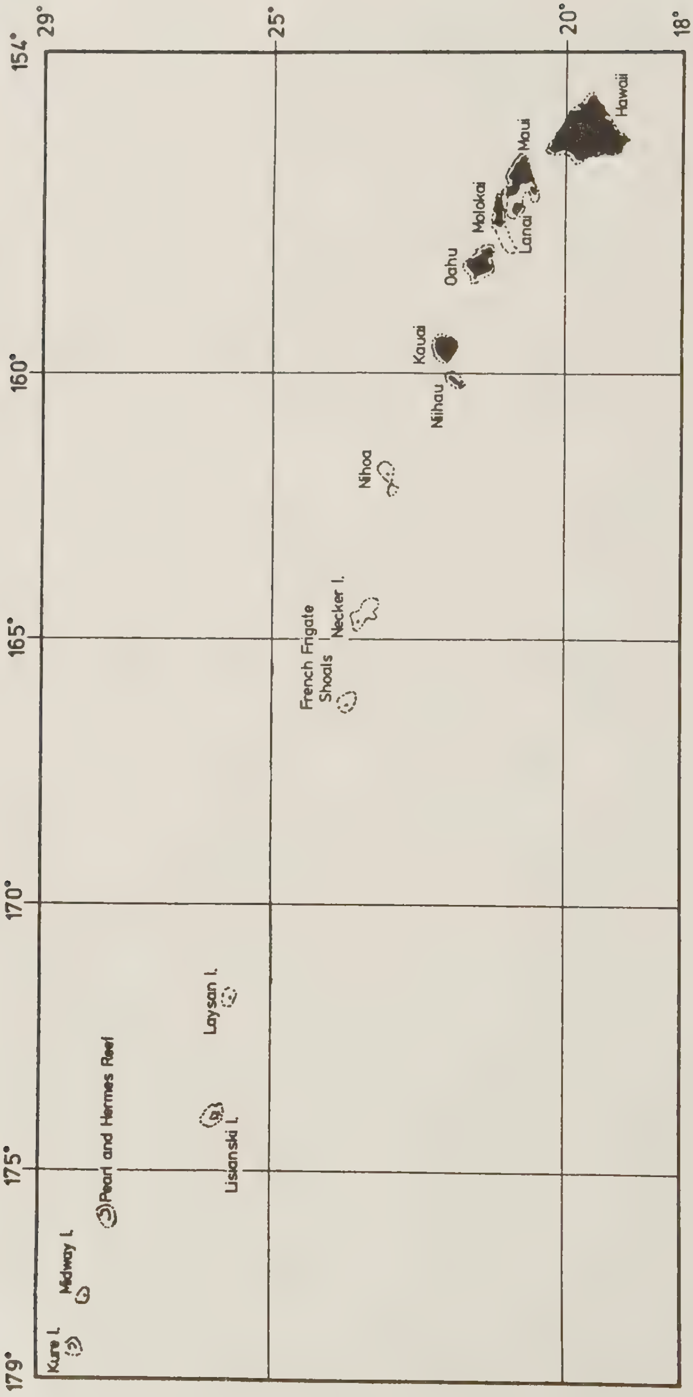
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Hawaii
Maui
Molokai
Lanai
Oahu
Kauai
Niihau
Nihoa
Necker I.
French Frigate Shoals
Laysan I.
Lisianski I.
Pearl and Hermes Reef
Midway I.
Kure I.

FIGURE 1. The Hawaiian Archipelago.

season. This report summarizes the current information on the "preferred" birth and postnatal nursing sites of Hawaiian monk seals in the NWHI and identifies the apparent characteristics of this preferred pupping habitat.

MATERIALS AND METHODS

The information used to identify the birth and nursing sites of monk seals from 1981 to 1988 in the NWHI was obtained from published reports and unpublished National Marine Fisheries Service (NMFS) data listed in Table 1. The descriptions of the sites were prepared from a combination of published and unpublished information, including photographs, maps, and charts; interviews with individuals familiar with the sites; and the authors' observations of these locations in recent years.

Much of the information on beach use by monk seals before 1981 does not contain details on birth sites. With few exceptions, field time was very short relative to the extended pupping season of monk seals. From 1977 to 1981, the entire pupping season or most of it was monitored at Laysan Island (Johnson and Johnson 1984). Beginning in 1981 at Kure Atoll and expanding to all other major breeding islands in the following years, the NMFS identified all observed birth sites and nursing locations by recording the appropriate sectors of the various islands. The sectors include all of the potential haul-out areas (places where seals come out of the water to rest, molt, give birth, etc.) on the permanent islands in the NWHI. Sectors are delineated by natural or man-made markings and may vary in size within and among the NWHI. The small, semipermanent sand-spit islets are not similarly partitioned; seals on these islets are simply noted as being present, without more specific information on location.

TABLE 1

DATA SOURCES ON RESEARCH CONDUCTED ON HAWAIIAN MONK SEALS IN THE NORTHWESTERN HAWAIIAN ISLANDS, 1982–1987

LOCATION	1982	1983	1984	1985	1986	1987
Necker Island	Conant (1985)	Morrow and Buelna (1985)	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)
French Frigate Shoals	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)
Laysan Island	Alcorn (1984)	Alcorn and Buelna (1989)	Johanos et al. (1987)	Johanos and Austin (1988)	NMFS (unpubl. data)	Becker et al. (1989)
Lisianski Island	Johanos and Henderson (1986)	Johanos and Kam (1986)	Alcorn et al. (1988)	Alcorn et al. (1988)	Westlake and Siepmann (1988)	—
Pearl and Hermes Reef	—	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	Forsyth et al. (1988)	NMFS (unpubl. data)
Kure Atoll*	NMFS (unpubl. data)	NMFS (unpubl. data)	NMFS (unpubl. data)	Reddy and Griffith (1988)	NMFS (unpubl. data)	Reddy (1989)

*Kure Atoll: 1981 data are from Gilmartin et al. (1986) and 1988 data are from NMFS (unpubl. data).

RESULTS AND DISCUSSION

The volume of data available on birth sites of monk seals in the NWHI varies among the island locations and years. These data were reported inconsistently by observers of Hawaiian monk seals from the late 1950s until 1977 at Laysan Island and 1981–1982 at other islands. Although all birth sites observed since 1981 have been documented, the pattern of field effort of the NMFS on the breeding islands has varied. Determination of pupping sites has been incidental to other NMFS monk seal research and recovery activities. Despite these limitations, all of the major breeding islands (with the exception of Pearl and Hermes Reef) since 1981 have had nearly full coverage of at least two pupping seasons in which dates and locations of all observed births were recorded. The available data from the late 1950s to the present do not indicate that these observed patterns have varied, except at Kure Atoll, where human disturbance has been an important factor (unpubl. data).

Locations of birth sites and first sightings of nursing mother-pup pairs (where pups were less than 1 week old), along with descriptions of these sites, are presented below, beginning at the eastern end of the NWHI.

Nihoa

The easternmost island of the NWHI is Nihoa Island, a 63-ha remnant of a precipitous volcanic peak with a maximum elevation of 273 m (Clapp et al. 1977). With few exceptions, the island's shoreline perimeter is steep lava cliffs. The west side has a large lava bench, and the westernmost cove on the south side has a small, sandy beach, known as Derby's Landing, that monk seals use as a haul-out and pupping area (Figure 2, *top*). Two other coves on the south side have small, rock terraces whose accessibility to the seals is dependent on tide and sea conditions. The cliffs along the north and east sides of Nihoa Island rise straight from the ocean, and only a few rocky outcroppings potentially can be used by the seals. The bottom along the entire shoreline drops off quickly.

Up to two weaned pups per year were sighted at Derby's Landing during brief visits from 1981 to 1986 (S. Conant, unpublished data). Observers have been on Nihoa Island for only 5 days or less in each of the last 5 yr, making it impossible to document well the number of births or birth locations. One mother-pup pair was seen each year in 1986 and 1987 at Derby's Landing (T. Gerrodette, pers. comm.). The very limited haul-out areas at Nihoa Island will keep this seal population small.

Necker Island

Necker Island also is a small (17 ha) remnant of volcanic rock with high, steep slopes (maximum elevation of 84 m) and has only a few rocky ledges that can be used by monk seals. The bottom along the entire perimeter of the island drops quickly to at least several meters deep.

Data on nursing pups at Necker Island were collected intermittently during 1982–1987, with coverage ranging from 1 day to 2 weeks each year (Table 2). Most mother-pup pairs were on the west side of Shark Bay in sector 5 (Figure 2, *bottom*). A basalt ledge with a few small tide pools at the shoreline, sector 5a appears to be the primary rookery and haul-out area, although no births have been witnessed. The water beyond the tide pools off sector 5a is at least 2 m deep, enough to allow sharks along the ledge. Although this area normally receives little wave action during the pupping season, waves can wash completely over this ledge during summer storms (WGG, personal observation). The few other haul-out sites for seals at Necker Island are much smaller and are predominantly used by adult males, which may discourage use of these areas for pupping. Ten of 11 mother-pup pairs were sighted in sector 5a during 6 yr of observations; the other pair was sighted in sector 8 in 1982 (Conant 1985). No nursing or weaned pups were seen during short trips to Necker Island in May of 1986 and 1987 (T. Gerrodette, pers. comm.). As at Nihoa Island, the limited haul-out space prevents Necker Island from becoming a major breeding site.

French Frigate Shoals

French Frigate Shoals, located about 930 km northwest of Honolulu, is a low-lying, multi-island coral atoll, which currently has the largest population of Hawaiian monk

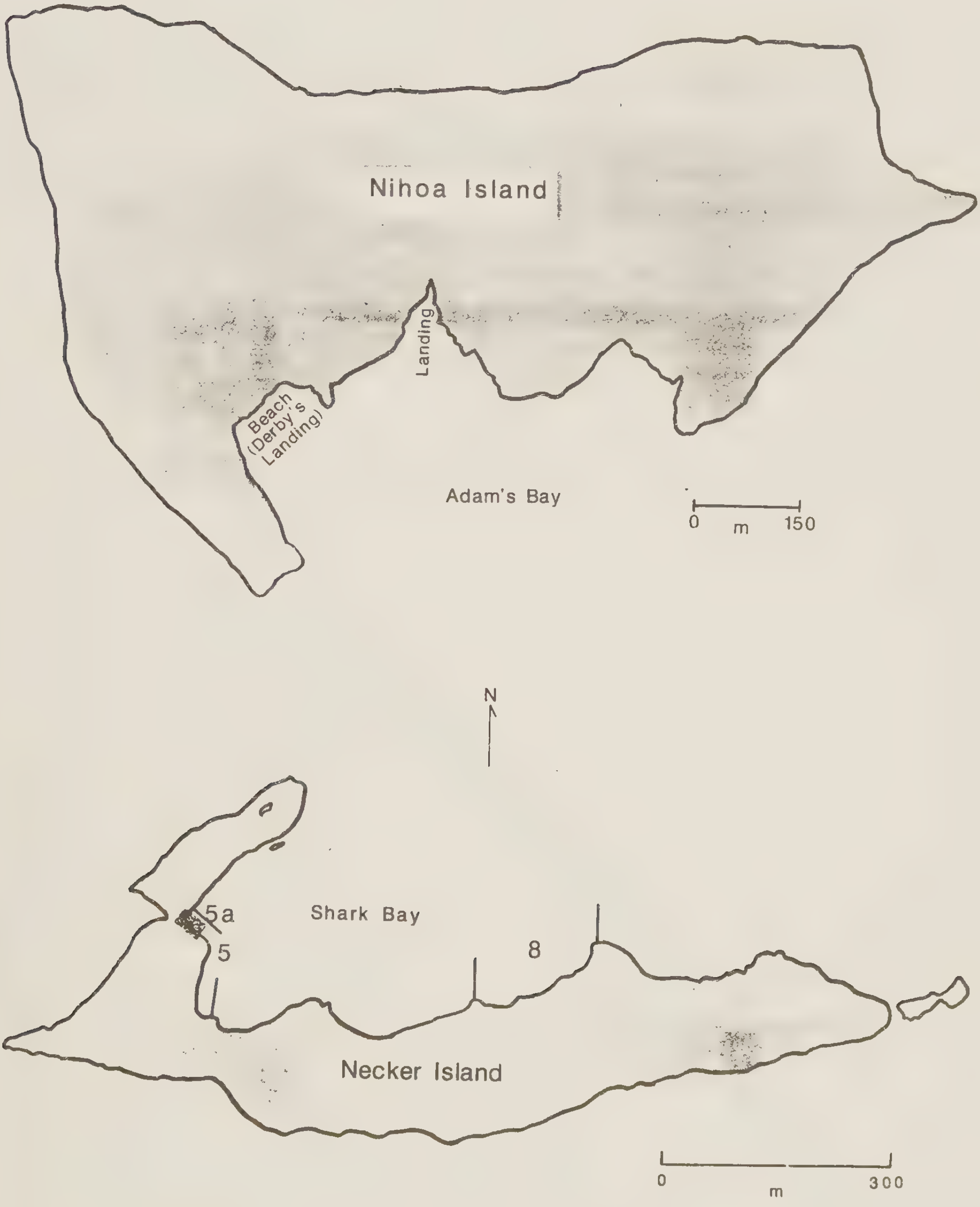
Nihoa Island
Landing
Beach (Derby's Landing)
Adam's Bay
0 m 150
N
Shark Bay
5a
5
8
Necker Island
0 m 300

FIGURE 2. *Top*, Nihoa Island; *bottom*, Necker Island (section 5a is darkened area).

TABLE 2

Necker Island Monk Seal Birth Locations

SECTOR	1982	1983	1984	1985	1986	1987	TOTAL
5	3	2	3	2			10
8	1						1
Total							11

Note: See Figure 2, *bottom*, for sector locations.

seals in the NWHI (Figure 3). The atoll is approximately 28 km across its longest axis and consists of 10 permanent or semiperminent islands and at least three small, sand-spit islets that are present intermittently, depending on weather and tide conditions. Pupping activity within the shoals occurs primarily on East, Whale-Skate, and Round islands, although some births are known to have occurred at most of the other islands as well.

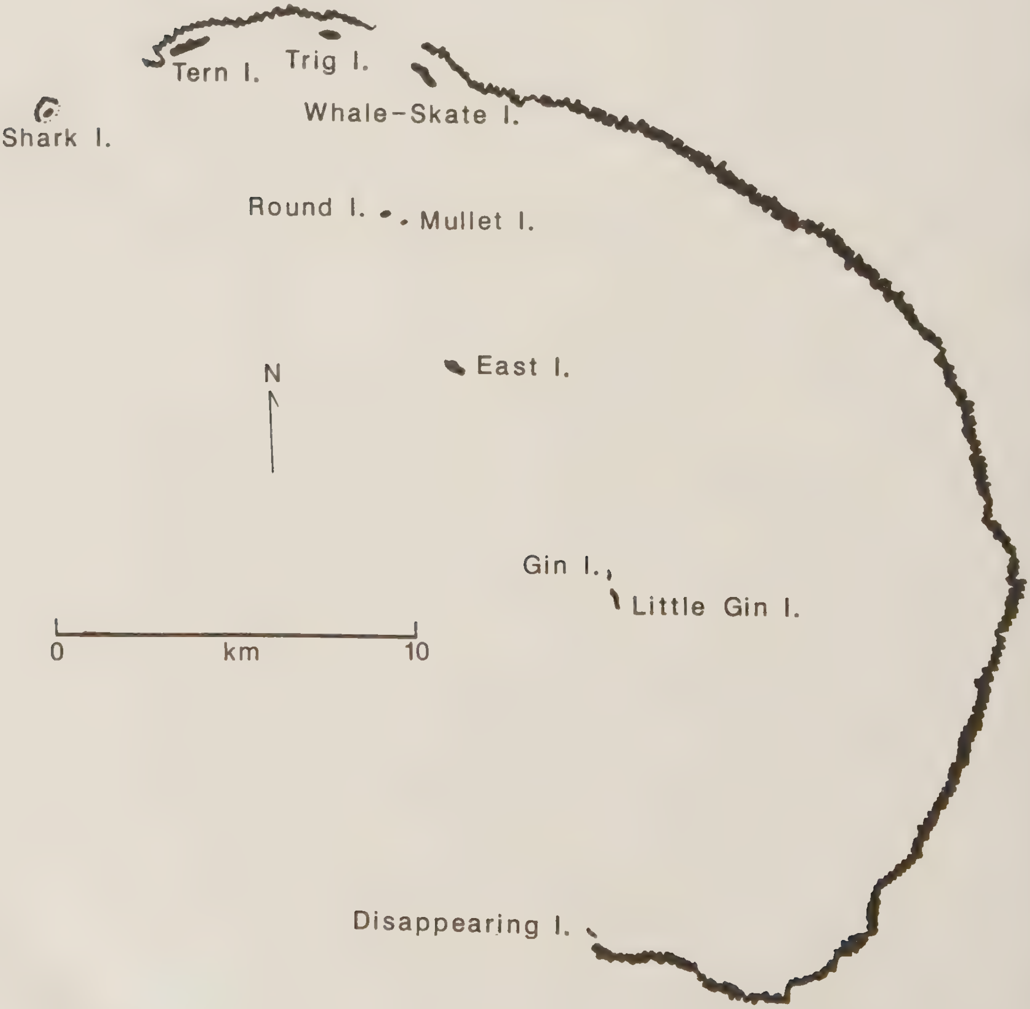
Tern I.
Trig I.
Shark I.
Whale-Skate I.
Round I.
Mullet I.
N
East I.
Gin I.
Little Gin I.
0
km
10
Disappearing I.

Figure 3. French Frigate Shoals.

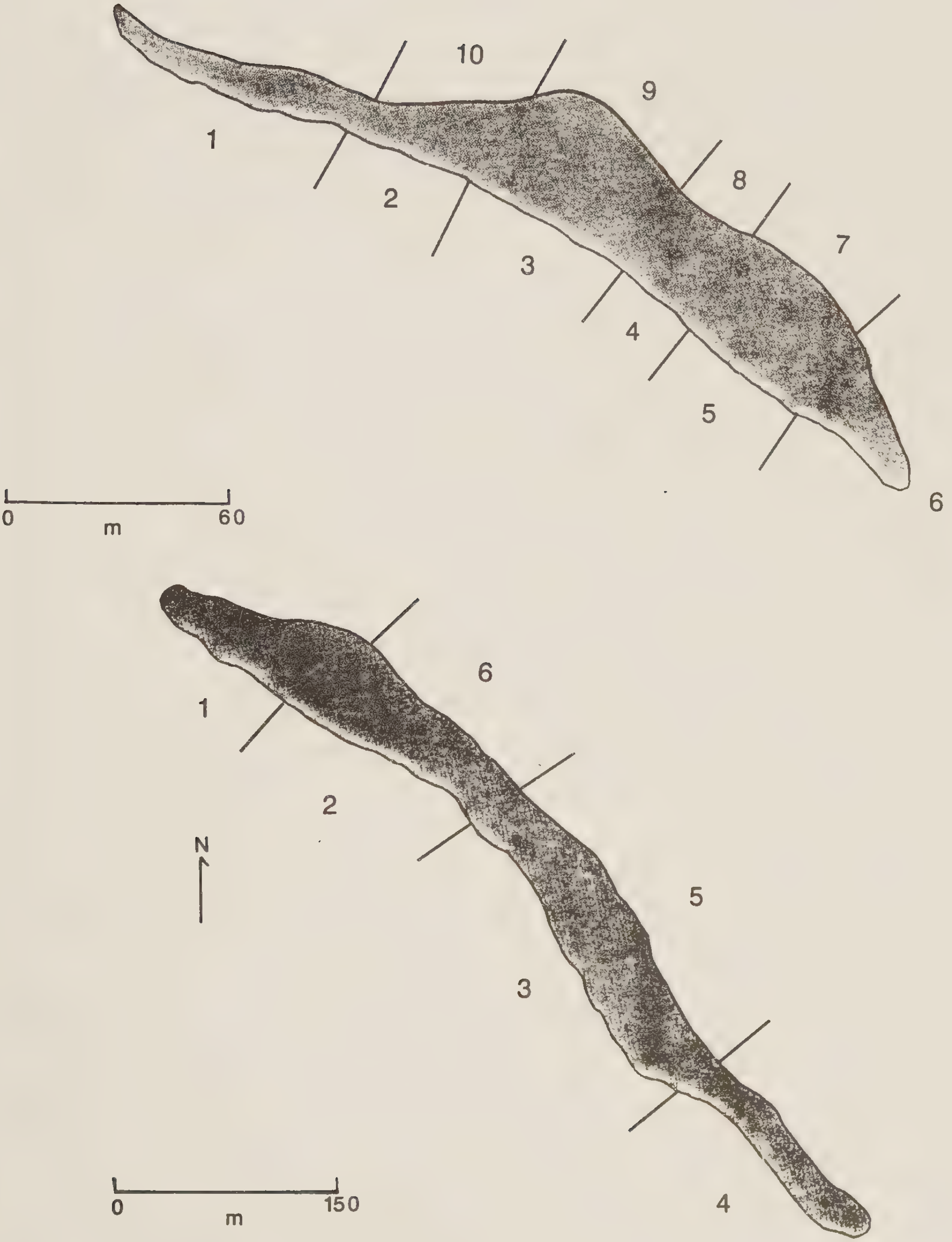
10
9
1
8
2
7
3
4
5
6
0
m
60
6
1
2
N
5
3
0
m
150
4

FIGURE 4. French Frigate Shoals: *top*, East Island; *bottom*, Whale-Skate Island.

East Island, near the center of the atoll, is the main pupping island of the monk seals (Figure 4, *top*; Table 3). It is an elongated island, 4.5 ha in size with an elevation of about 2 m, and lies within the inner crescent-shaped reef. It has a low vegetation cover consisting of grasses, vines, and shrubs. Some ruins of a U.S. Coast Guard (USCG) loran station, built in 1944 and abandoned in 1952, are scattered about the island.

After the USCG left East Island, mother-pup pairs were frequently sighted on its southwest beach, increasing in numbers during the rapid growth of the FFS population in the 1960s (Amerson 1971). Beginning in 1983, births have been monitored closely at East Island by NMFS. Data since 1983 show that about one-half of the births at FFS and at least one-fourth of the births in the entire NWHI occur at East Island.

East Island is divided into 10 sectors: sectors 1 and 6 on the west and east tips of the island, respectively; sectors 2–5 on the southwest side (leeward); and sectors 6–10 on the northeast (windward) side (Figure 4A). Almost all mothers with newborn nursing pups on East Island (96% of 177 sightings) were found on the beaches at the east or west tip of the island, sectors 1 and 6, and along the south shore, sectors 2–5 (Table 3). The south side of the island is paralleled by a very shallow, wide reef flat. The shallow water offers protection from shark intrusion into the swimming area of the mother-pup pairs. Only a small portion of the north side of East Island is similarly abutted by shallow reef. Most of the sandy shoreline on the north side drops off quickly and is patrolled regularly by large tiger sharks, *Galeocerdo cuvieri*, during the early summer months.

East Island also has relatively few adult male seals during the breeding season. Adult males in search of females in estrus can be a continuing disturbance to mother-pup pairs, as some posturing and vocalizing on the part of the female is necessary to cause the male to stop pursuit. Absence of this disturbance may also contribute to making East Island a preferred pupping island.

The other frequently used pupping islands at FFS are Whale-Skate and Round islands. If combined, the births at these two islands equal about 60% of those at East Island. Whale-Skate Island is 6.8 ha of coral rubble and sand, with vegetation similar to that at East Island. Whale-Skate Island lies along the northern shelf of the reef; is long, narrow, and slightly curved; and has an elevation maximum of about 2 m (Figure 4, *bottom*).

From 1983 to 1987, 107 sightings of births and newborn pups on Whale-Skate Island were made; the distribution clearly favored sectors 1, 2, 3, and 6 (Table 3), the northwest end and southwest beach (Figure 4, *bottom*). Many large coral heads are scattered near shore around the northwest half (sectors 1 and 6) of the island. The water over the reef is very shallow, and throughout the area is a maze of narrow channels of water 2–3 m deep. The beach at the northwest end is 10–15 m wide and has vegetation behind the berm. Sectors 2 and 3, also frequently used for pupping, are on the south side (leeward) of the island. This

TABLE 3

French Frigate Shoals Monk Seal Birth Locations

SECTOR	1983	1984	1985	1986	1987	TOTAL
East Island						
1	2	8	4	6	5	25
2	2	7	5	3	5	22
3	3	5	7	6	13	34
4	3	6	2	13	8	32
5	1	2	8	7	8	26
6	6	7	5	7	6	31
8		1				1
9	1	1		1	1	4
10				2		2
Total						177
Whale-Skate Island						
1	5	5	8		5	23
2	2	4	5		10	21
3	3	5	5	4	6	23
4		2	2	1	2	7
5	1	4	1	2	1	9
6	5	8	4	3	4	24
Total						107
Round Island		25	21	14	21	81
Little Gin Island		7	3	3	6	19
Trig Island		3	1		1	5
Tern Island		1*	1*	2*	2*	6
Other islands: Mullet, Disappearing, Gin		4	1	5	12	22

Note: See Figures 3–4 for island and sector locations.
* Premature or stillbirths.

latter area has a narrow channel about 1 m deep along the beach with a shallow reef 30 m wide adjacent to it. Females giving birth in sectors 2 and 3 selected sites with the shallowest water. Sectors 4 and 5 on the opposite side of the narrow island have deeper water and less reef protection along the shore.

The third major pupping site is Round Island, a small, sandy, nonvegetated islet with a maximum area of about 0.1 ha and an elevation that does not exceed about 1.5 m. It is almost completely surrounded by very shallow water and reef. Numerous mother-pup pairs have been observed at Round Island since 1956 (Amerson 1971; Table 3). It is much smaller than East and Whale-Skate islands, and it has the highest density of mother-pup pairs. But despite the high density at Round Island during the pupping season, adult females prefer to use it rather than other small sand-spit islets that lack its protective reef, shallow-water perimeter, and stability (Round Island rarely disappears).

A small number of mother-pup pairs have been recorded on other islands within FFS (Table 3), most of which have little or no vegetation because they are periodically awash in the winter. Little Gin Island (Figure 3) lies southeast of East Island in the crescent-shaped reef and is about 2 ha of sand with a very small area of vegetation. The water along the shoreline is at least 1 m deep. Mother-pup pairs have been sighted on Little Gin Island since the late 1950s, but in relatively few numbers compared with these on East, Whale-Skate, and Round islands (Amerson 1971). Births continue to be observed here, averaging five per year. A few other small sand islets, Mullet, Disappearing, Trig, and Gin Islands (Figure 3), combined contribute about seven pups per year. These locations have water at least 1 m deep along the shoreline and may disappear easily with changes in weather, tide, and current patterns.

The largest land mass in the shoals is Tern Island (Figure 3), a 14-ha man-made island completed in 1942 as an aircraft refueling site (Amerson 1971), with an elevation of 2 m. It has been nearly continuously occupied by humans, but an important change for monk seals occurred in 1979: the USCG loran station, which had been relocated from East Island to Tern Island in 1952, was closed, and the U.S. Fish and Wildlife Service (USFWS) began occupation of the island. Before this change, Tern Island was used only occasionally by monk seals, but since 1979 the annual mean beach counts have risen dramatically, to 80–90 seals in recent years. This increase occurred because of a change in beach use: access by station personnel is now highly restricted, and no dogs are present on the island.

The entire south beach of Tern Island is suitable for hauling out and is heavily used by seals for resting and molting, but observers have recorded only a few stillbirths and premature births on Tern Island between 1979 and 1987 (Table 3). Some readily identifiable adult female seals have used Tern Island regularly for hauling out and then, within a few days of a Tern Island sighting, appeared on East Island with a newborn pup. Tern Island provides a haul-out beach near the windward atoll slope and fringing reef, which is probably good foraging habitat at FFS. The cause of the premature and stillbirth incidents that occur on Tern Island is not understood, but may be related to these females not receiving sufficient physiological warning of the imminent births and, therefore, not seeking a more appropriate parturition site.

Tern Island will probably not become a major pupping island for monk seals because of the surrounding water habitat. The water along the beach becomes deep quickly, and the offshore reef does not provide a sufficient barrier to dissipate waves from the south nor prevent the access of large sharks to the near-shore area. Large sharks have been observed swimming close to this shoreline, making it incompatible with high pup survival (K. W. Kenyon and M. J. Rauzon, unpubl. data, 1977).

Laysan Island

The largest island in the NWHI is Laysan Island, about 365 ha, which contains a large hypersaline lake in its central depression (Figure 5, *left*). The highest elevation is just over 12 m. Laysan Island is divided into 20 sectors, is well vegetated with a variety of plant life, and has some wide (200–400 m), sandy

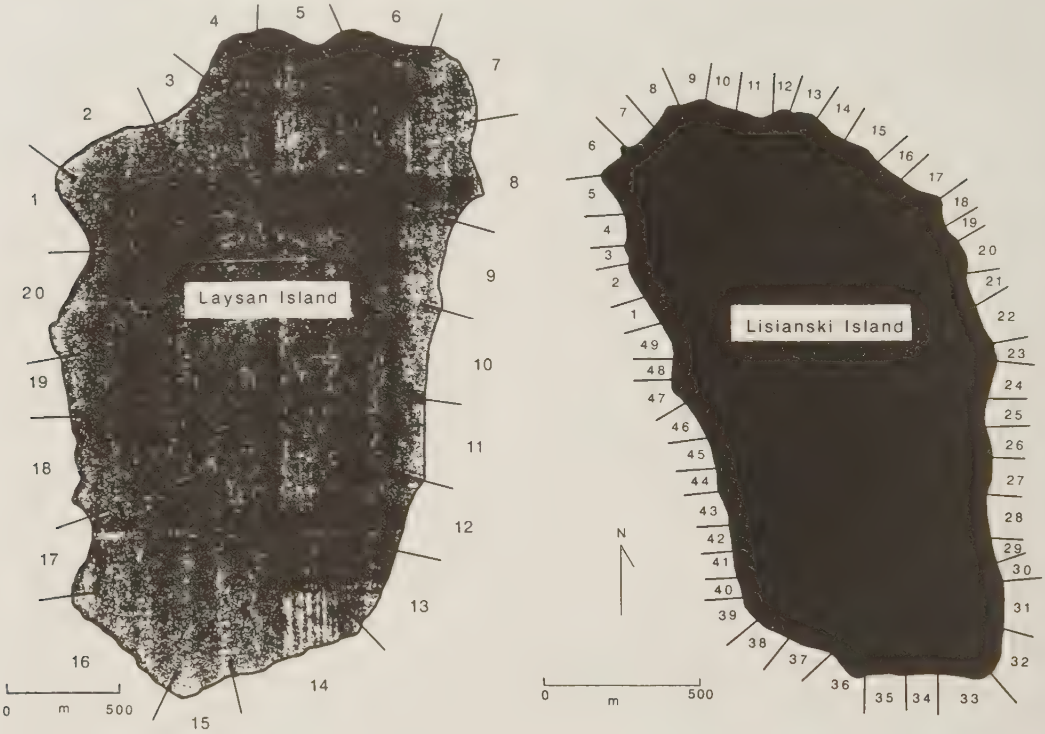

Figure 5. *Left*, Laysan Island; *right*, Lisianski Island.

beaches on the north side (sectors 4–10) (Ely and Clapp 1973). The beaches on the northwest and west sides of the island, sectors 1–3 and 17–20, are narrower (50–200 m) and steeper and have vegetation at the berm. The nearshore areas on the west and northwest sides (sectors 18–20 and 2–3) consist of extensive reef flats, which are exposed most of the time. Present along this shoreline are rocky ledges that provide small pools of shallow water. Large waves break up on the fringing reef, 100 m or more from the beach.

During 1977–1980, most of the pupping (76%) occurred at the northwest quarter of the island (Johnson and Johnson 1984). This pattern continued during 1982–1987, based on information on the birth locations of 104 pups at Laysan Island. About 55% of the births occurred in sectors 2–3 and 19–20, and 66% of the total number occurred in the northwest quarter (Table 4).

Sectors 10–13 on the east side of the island were the site of 17 (16%) of the known births at Laysan Island in 1982–1987. This area is very calm and shallow (1.0–1.5 m), with a prominently exposed coral-rock border that parallels the shoreline and is, on average, about 100 m offshore. Few adult males searching for females frequent this area, so mother-pup pairs remain relatively undisturbed while swimming near the beach. The beach is very wide here, up to 75 m, and mother-pup pairs have not been seen using the inland vegetation.

Not commonly used for pupping are those areas along the south shore and northeast side of the island. A large coral shelf drops into deep, choppy water on the south side in sectors 15 and 16. Along the northeast shore (sectors 6–8), tradewinds can create extremely rough surf on the beaches and can cause sand storms. Also, the very wide northeast beach requires a mother-pup pair to travel up to 400 m to reach vegetation for protection from inclement weather.

Most pupping activity at Laysan Island co-

TABLE 4

LAYSAN ISLAND MONK SEAL BIRTH LOCATIONS

SECTOR	1982	1983	1984	1985	1986	1987	TOTAL
1			1	1		2	4
2	5	3	4	6	1	2	21
3	1		1	4	1	2	9
4	1		1		1		3
5	1		1	1		2	5
6			1	1	1	1	4
7			1				1
8			1	1			2
10	1		1		1		3
11	1	2	2	3		1	9
12				1		1	2
13	1					2	3
18			1	1	3	1	6
19	2	2	1				5
20	9	2	2	6	2	6	27
Total	22	9	18	25	10	20	104

NOTE: See Figure 5, *top*, for sector locations.

incides temporally with the seasonal, nonaggressive aggregations of gray reef sharks, *Carcharhinus amblyrhynchos*, in the shallow waters off sectors 2 and 3. Seals have been seen swimming through these large aggregations without incident (Alcorn and Buelna 1989).

Lisianski Island

Lisianski Island is a low coral and sand island situated at the northern edge of Neva Shoal (Clapp and Wirtz 1975). It is 182 ha, with a maximum elevation of just over 6 m. The top of the island is densely covered with shrubs and grasses. Most beach areas around the island (except the southeast) are sloped, relatively narrow (about 10–15 m wide), and backed by abundant vegetation behind the berm. The shoreline along most beaches drops off quickly to 1 m or more in depth; only occasionally are the beaches abutted by shallow reef. The island has been divided into 49 sectors for recording seal sightings (Figure 5, *right*).

The mideastern beach is primarily low, rocky ledges with small tide pools, expanding to wider (100–150 m), flat, sandy beaches toward the south end of the island. Sector 28 (Figure 5, *right*) contains a rocky ledge at the shoreline and has a coral ridge 3–5 m from the beach that is exposed at low tide. The coral ridge parallels the beach, forming a shallow channel alongshore. The beach here is slightly sloped and ca. 15 m wide. At the beach crest, large clumps of bunchgrass (*Eragrostis variabilis*) and other vegetation provide shelter for seals from wind and rain. At the waterline of sectors 23–25 is a coral ledge that creates pools protected from the deeper water. The entire ledge runs parallel to the shoreline and slopes up above the water into dense vegetation that climbs farther up a steep embankment. The protected, shallow shoreline beaches of sectors 23–29 provide the only large area of this type of habitat at Lisianski Island.

Although coverage of the island by NMFS personnel during the field seasons varied greatly from 1982 to 1986 (no data for 1984 or 1987), it is evident from the data that births are most concentrated on the southeast beaches (Table 5). Of the 33 known birth and neonatal sightings recorded in 4 yr, 17 occurred in sectors 23–29. Sector 28, about 2% of the island's perimeter, was clearly the pre-

TABLE 5

LISIANSKI ISLAND MONK SEAL BIRTH LOCATIONS

SECTOR	1982	1983	1984	1985	1986	TOTAL
2	1					1
5		1				1
11	1					1
12		1				1
13				1		1
17	1					1
19					1	1
20	1					1
21					1	1
23	1					1
24	1					1
25	1	1				2
27	1					1
28	5	3		1	1	10
29	2					2
31		1				1
32	1					1
36	1					1
39	1					1
40		1				1
43		1				1
44		1				1
Total						33

NOTE: See Figure 5, *bottom*, for sector locations.

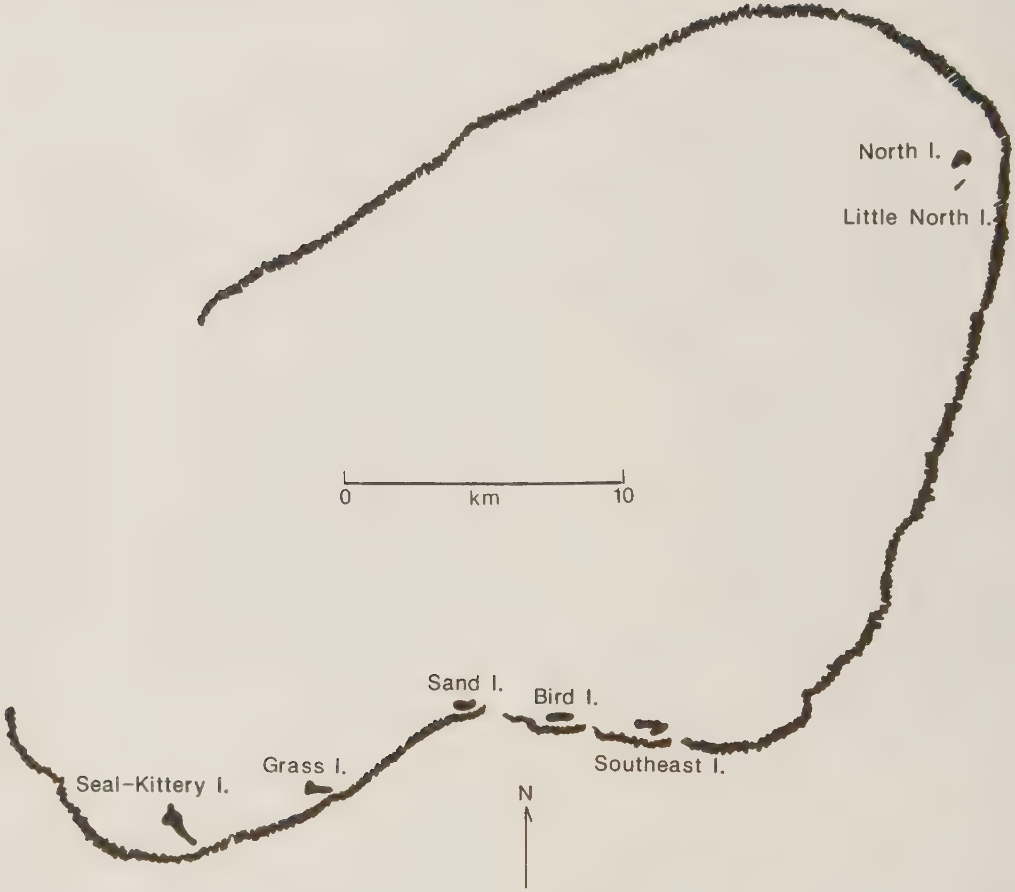

Figure 6. Pearl and Hermes Reef.

ferred area overall, with 10 (30%) of the known births occurring there. Additional sightings of older nursing pups at first arrival of field camps indicate that sector 20 is also an important nursery habitat.

Pearl And Hermes Reef

Pearl and Hermes Reef usually consists of seven small islands and their associated sand spits (Figure 6). Only four of the islands have vegetation above all or some of the beaches. The atoll is ca. 32 km wide, and the fringing reef has a wide opening at the west end and several smaller channels through the reef along the south side.

The northernmost islands within the atoll are North Island, with its associated sand spits, and Little North Island, a few hundred meters southeast of North Island (Figure 7). These two islands are separated by a channel 3–4 m deep. North Island is a vegetated, comma-shaped island with gradually sloping, sandy beaches and a sand spit extending southward off the west side. Depending on the tide and the season, a variable number of small sand islets in shallow water emerge off North Island's south tail and provide haul-out space for seals. Little North Island is a long, narrow sand spit lacking vegetation and frequently changing in size and shape.

Of the 35 observed births and mothers with newborn pups at Pearl and Hermes Reef, 30 (86%) were seen on these two northernmost

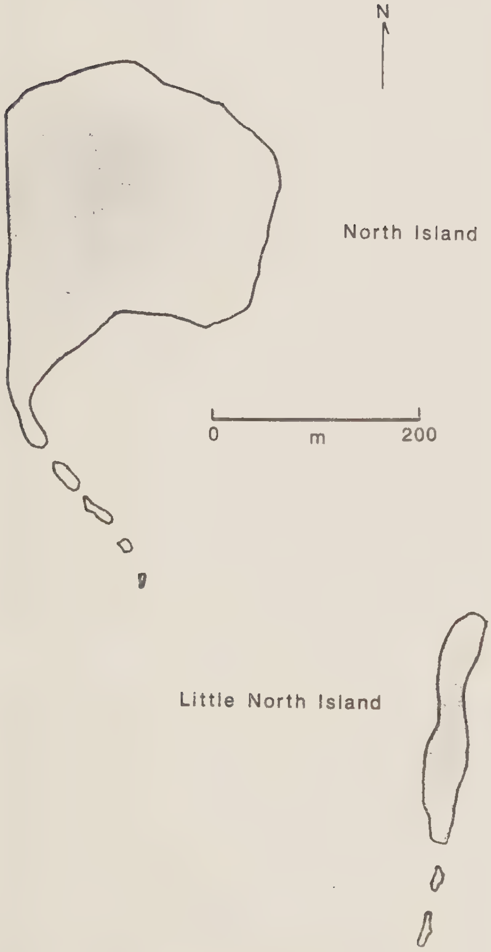

FIGURE 7. North and Little North Islands, Pearl and Hermes Reef.

islands, with the majority of pairs using the west shore of North Island and its spit islets (Figure 7, Table 6). Most of the mother-pup pairs on Little North Island also appeared along the west (leeward) side. The calm and very shallow (<0.5 m deep) leeward waters cover an extensive area near shore. Mother-pup pairs using the exposed sand islets off the southern tip of North Island have been observed to move between these islets (WGG, personal observation). The water is also very shallow (≤0.5 m) around these islets and may be formed into small, stagnant pools by the sand. Large tiger sharks have been seen in the deep channel that separates Little North Island from North Island, and no movement of mother-pup pairs across the channel has been documented.

The islands at the south end of the atoll are farther apart (1–2 nmi) and are surrounded by water along the beaches that becomes deep (1–2 m) quite rapidly. Although mother-pup pairs have occasionally been seen on Bird Island, Southeast Island, and Seal-Kittery Island, they constitute a small percentage (14%) of the total births observed at Pearl and Hermes Reef.

Midway Islands

Monk seals once occupied Midway Islands (Figure 1) in high numbers, with beach counts exceeding 70 animals, but the population was nearly eliminated in the 1960s and 1970s because of human disturbance and has yet to show signs of recovery (Kenyon 1972,

TABLE 6

PEARL AND HERMES REEF MONK SEAL BIRTH LOCATIONS

LOCATION	1983	1984	1985	1986	1987	TOTAL
North Island and sand spits	4	2	4	7	8	25
Little North Island	3	2				5
Southeast Island		1		1		2
Bird Island	1		1			2
Sand Island						—
Grass Island						—
Seal-Kittery Island	1					1
Total	9	5	5	8	8	35

NOTE: See Figures 6 and 7 for island locations.

Johnson et al. 1982). NMFS and USFWS personnel have attempted to monitor Midway Islands for pupping activity since 1980 with intermittent visits annually. During that time, an average of less than one pup per year has been born on Eastern Island and the sand islets between Eastern and Sand islands, the atoll's two major islands. Because of the very low number of births, the uncertainty of the exact birth locations (no births were witnessed in the last decade), and the possibility that human disturbance still influences birth site selection, preferred monk seal birth sites at Midway Islands are not discussed here.

Kure Atoll

Kure Atoll, about 2220 km from Honolulu, is the westernmost atoll in the NWHI and also the northernmost coral atoll in the world (Figure 1, 8). The atoll consists of a large (130 ha), permanently vegetated island, Green Island (Figure 8), and up to three small sand islets, the size and presence of which are dependent upon the current and weather. Green Island has a maximum elevation of 7.5 m, and the beaches are backed by a very dense, deep cover of *Scaevola taccada*. Sandy beach projections at both ends of Green Island change slightly with the weather and seasons (Woodard 1972). Sand Island, the largest and most stable of the sand islets, may be up to 20 m wide and 200–300 m long.

In 1961, the USCG began operation of a 20-person loran station on Green Island, where almost all monk seal births had occurred. Thereafter, the preferred pupping sites on Green Island were abandoned under the pressure of human disturbance, and the seals began to use the sand islets to give birth and rear their pups. This resulted in an increase in pup mortality, a slow decline in beach counts of seals because of little or no recruitment, and then decreasing numbers of births (Kenyon 1972, Gerrodette and Gilmartin, in press). These changes were attributed to human disturbance, which included harassment by dogs and vehicles driven on the beaches.

In 1976, the USCG made several changes in the beach-use policy at Kure Atoll to reduce impact on monk seals, and this began to slowly reverse the changes that had occurred in haul-out patterns. An off-limits area was designated at the north end of Green Island, dogs were removed from the island, recreational use of vehicles on the beaches was prohibited, and the sand islets were placed off limits. These actions gave the seals some relief and refuge from human activities, and in time births resumed on Green Island (Gerrodette and Gilmartin, in press). In 1981, NMFS began an intensive field program at Kure Atoll in an attempt to increase pup survival. This work focused on the temporary captive maintenance of female pups after weaning (Gilmartin et al. 1986) and on monitoring USCG beach activities.

In 1981, six of 10 Kure Atoll pups were born on Green Island beaches and the other four were born on Sand Island. From 1981 through 1984 the births on Green Island occurred on all beaches except sector 8, which is the primary USCG recreational beach. Beginning in 1985, birth sites have been almost exclusively (15 of 18 births) limited to sectors 5–7 (Table 7), the west point of the island with beaches 15–30 m wide, and the sand bar extending off sector 6. The nearshore water off these sectors is shallow, with a coral and sand bottom. The topography along sectors 3–4 is similar to that at sectors 5–7, but the east beach area has not been used in recent years for pupping. Sector 2 is the off-limits beach on the island, and although it has been the most used by seals for resting and molting, only five births have occurred there in 4 yr. The bottom along the shore on the west side (sectors 1–2 and 8) drops off quickly to a sandy bottom 1–2 m deep. From 1982 to 1989, 31 of 33 pups were born on Green Island.

The locations selected by Hawaiian monk seals for parturition are not randomly distributed along the beaches available to them. At all of the breeding locations (except Necker and Nihoa islands) up to about 10 km of beach could be used for giving birth, but the distribution of pupping is actually very limited to relatively short shoreline distances. These particular areas also appear to be used repeatedly by parturient females over periods

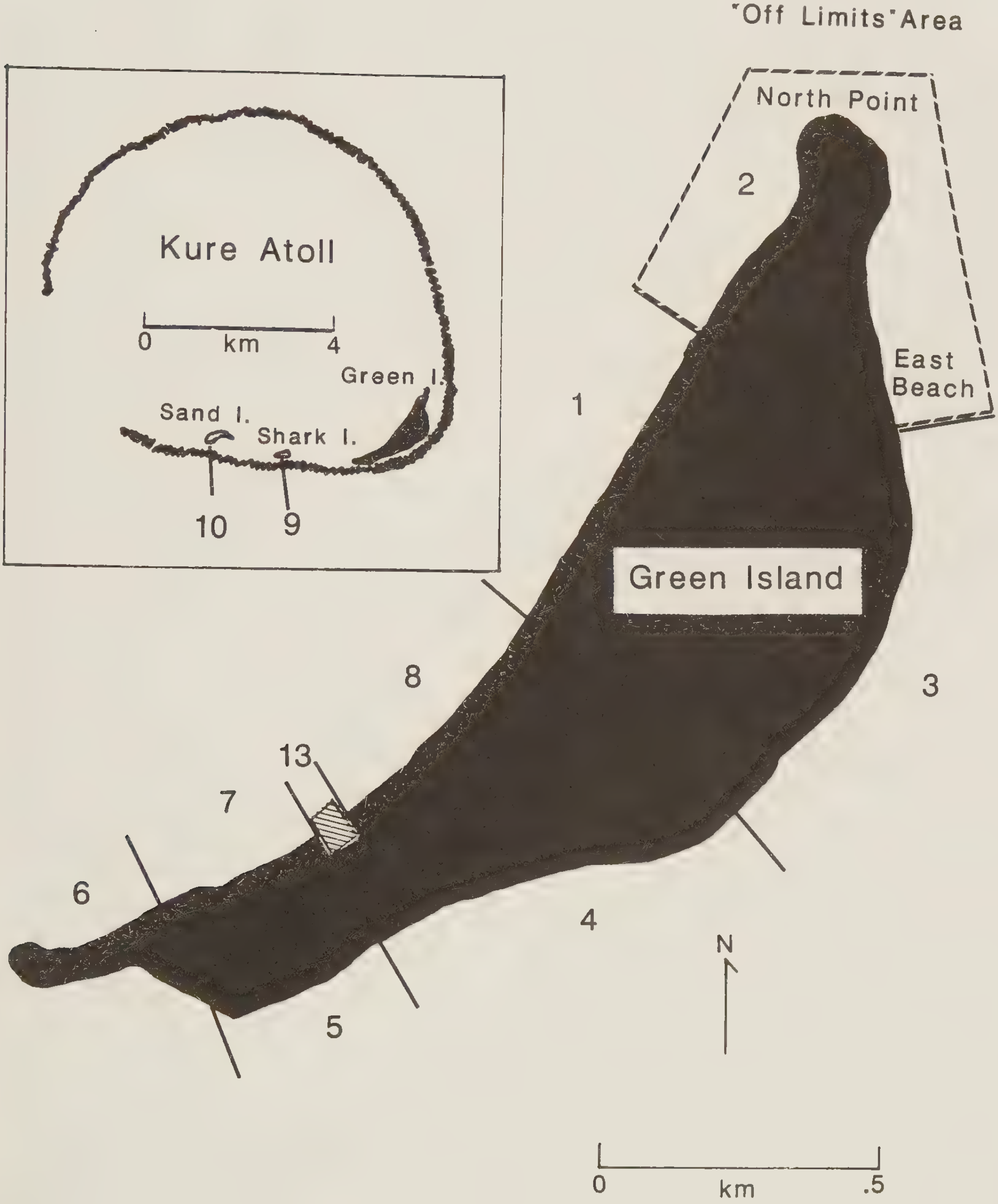
"Off Limits" Area
North Point
2
East Beach
1
3
Green Island
8
13
7
6
4
5
N
0 km .5
Kure Atoll
0 km 4
Green I.
Sand I.
Shark I.
10
9

FIGURE 8. Kure Atoll (inset) and Green Island (sector 13 is the fenced pup enclosure).

TABLE 7

Kure Atoll Monk Seal Birth Locations

SECTOR	1981	1982	1983	1984	1985	1986	1987	1988	TOTAL
Green Island									
1	1	1							2
2		1	1	1				2	5
3	1			3					4
4	1								1
5		1		2	1		1		5
6	2		2		2	1		5	12
7	1	2			2		2	1	8
Subtotal									37
Sand Island									
	4			1			1		6
Total									43

Note: See Figure 8 for sector locations.

lasting at least several years. Although some mother-pup pairs may move 400–500 m along the shore during the nursing period (Alcorn 1984), they do not normally move beyond or between these protected beach areas.

These preferred pupping beaches have some similar characteristics. The primary attribute seems to be very shallow water along the beach. Also favored are sites with coral ridges or large rocks near the shoreline. They may fully or partially restrict shark entry to the water used by the mother-pup pairs during the day. These features, on either side (windward or leeward) of a permanent, vegetated island, seem to be highly attractive to Hawaiian monk seals about to give birth. A birth site with these beach characteristics should enhance survival of a pup through nursing and the early postweaning period, before the pup starts to move away from its natal beach.

Human disturbance in the past has caused monk seals to abandon preferred pupping and nursing sites, resulting in decreased pup survival. Several important birth sites have been described in this paper: Nihoa Island (Derby's Landing); Necker Island (sector 5a); at FFS, East Island (sectors 1–6), Whale-Skate Island (sectors 1–3, 6), and Round Island; Laysan Island (sectors 2–3, 11, 18–20); Lisianski Island (sectors 20, 25, 28–29); at Pearl and Hermes Reef, North Island (west side and spit islets) and Little North Island; and at Kure Atoll, Green Island (sectors 5–7). Recovery of the Hawaiian monk seal population is linked to protection of these areas from any disturbance that may cause monk seals to seek less satisfactory beaches for giving birth and nursing their pups.

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LITERATURE CITED

Alcorn, D. J. 1984. The Hawaiian monk seal on Laysan Island: 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-42. 37 p.

Alcorn, D. J., and E. K. Buelna. 1989. The Hawaiian monk seal on Laysan Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-124. 46 p.

Alcorn, D. J., R. G. Forsyth, and R. L. Westlake. 1988. Hawaiian monk seal research on Lisianski Island, 1984 and 1985.

U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-120. 22 p.

Amerson, A. B. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Res. Bull. 150. 383 p.

Becker, B. L., R. J. Morrow, and J. K. Leialoha. 1989. Censuses and interatoll movements of the Hawaiian monk seal on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-135. 25 p.

Clapp, R. B., and W. O. Wirtz, II. 1975. The natural history of Lisianski Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 186. 196 p.

Clapp, R. B., E. Kridler, and R. R. Fleet. 1977. The natural history of Nihoa Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 207. 147 p.

Conant, S. 1985. Observations of Hawaiian monk seals on Necker Island, Northwestern Hawaiian Islands. ‘Elepaio 46(2): 11–12.

Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 171. 361 p.

Forsyth, R. G., D. J. Alcorn, T. Gerrodette, and W. G. Gilmartin. 1988. The Hawaiian monk seal and green turtle on Pearl and Hermes Reef, 1986. U.S. Dep. Commer., NOAA Tech. Memo NMFS, NOAA-TM-NMFS-SWFC-107. 24 p.

Gerrodette, T., and W. G. Gilmartin. Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. Conserv. Biol. (in press).

Gilmartin, W. G., R. J. Morrow, and A. M. Houtman. 1986. Hawaiian monk seal observations and captive maintenance project at Kure Atoll, 1981. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-59. 9 p.

Johanos, T. C., and S. L. Austin. 1988. Hawaiian monk seal population structure, reproduction, and survival on Laysan Island, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-118. 38 p.

Johanos, T. C., and J. R. Henderson. 1986. Hawaiian monk seal reproduction and injuries on Lisianski Island, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-64. 7 p.

Johanos, T. C., and A. K. H. Kam. 1986. The Hawaiian monk seal on Lisianski Island: 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-58. 37 p.

Johanos, T. C., A. K. H. Kam, and R. G. Forsyth. 1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-70. 38 p.

Johnson, A. M., and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. ‘Elepaio 44(2): 43–45.

Johnson, A. M., R. L. Delong [sic], C. H. Fiscus, and K. W. Kenyon. 1982. Population status of the Hawaiian monk seal (*Monachus schauinslandi*), 1978. J. Mammal. 63(3): 415–421.

Johnson, B. W., and P. A. Johnson. 1984. Observations of the Hawaiian monk seal on Laysan Island from 1977 through 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-49. 65 p.

Kenyon, K. W. 1972. Man versus the monk seal. J. Mammal. 53:687–696.

Kenyon, K. W., and D. W. Rice. 1959. Life history of the Hawaiian monk seal. Pac. Sci. 13:215–252.

Morrow, R. J., and E. K. Buelna. 1985. The Hawaiian monk seal and green turtle on Necker Island, 1983. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-55. 11 p.

Reddy, M. L. 1989. Population monitoring of the Hawaiian monk seal, *Monachus schauinslandi*, and captive maintenance project for female pups at Kure Atoll, 1987. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-123. 37 p.

Reddy, M. L., and C. A. Griffith. 1988. Hawaiian monk seal population monitoring, pup captive maintenance program, and incidental observations of the green turtle at Kure Atoll, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-101. 35 p.

Schreiber, R. W., and E. Kridler. 1969. Occurrence of an Hawaiian monk seal (*Monachus schauinslandi*) on Johnston Atoll, Pacific Ocean. J. Mammal. 50(4): 841–842.

Westlake, R. L., and P. J. Siepmann. 1988. Hawaiian monk seal and green turtle research on Lisianski Island, 1986. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-119. 18 p.

Woodard, P. W. 1972. The natural history of Kure Atoll, Northwestern Hawaiian Islands. Atoll Res. Bull. 164. 318 p.

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Acoustic Measurement of Micronekton Distribution over Southeast Hancock Seamount, Central Pacific Ocean

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ABSTRACT

Acoustic detection of scattering layers over certain seamounts demonstrates significant diel variations that suggest changes in biological activity. We describe the behavior of these acoustic scattering layers over the Southeast Hancock Seamount in the central Pacific Ocean in 1985-88. Ground truth provided by sampling with midwater trawls provides a description of the organisms responsible for this scattering, but avoidance of the trawls by larger organisms may bias these results in certain circumstances. The spatial distribution of micronekton, as revealed by analysis of acoustic data, may differ from night to night; preliminary acoustic Doppler current profiler data indicate that ocean currents affect these distributions. The high density of the scattering layers may also bias acoustic measurements of ocean currents.

INTRODUCTION

Current-topography interactions result in complexities in physical oceanography [1] that can have important biological implications [2]. Increased biological abundance in regions near seamounts and islands is evident as increased acoustic scattering intensity as compared with open ocean waters [3]. Analysis of the temporal and spatial distributions of these scattering layers may depend upon geographic region, depth of seamount, and ocean current conditions. Acoustic scattering over certain seamounts may be characterized by diel variations of immense magnitude; many of these organisms are specific to these seamounts [4, 5, 6]. On shallower banks, however, the main acoustic scattering layers may be derived from oceanic regions and can be depleted by predators on the banks [7, 8]. Because seamounts represent a major geological feature of most ocean basins [9], these acoustic signatures may be widespread. Further, the variation in ocean currents and local oceanography induced by current-topography interactions [1] may result in corresponding variations in the characteristics of acoustic scattering at a particular seamount. In this paper, we describe diel variation in acoustic scattering over the Southeast Hancock Seamount, the abundance of micronekton organisms as determined by net sampling and acoustic signals, and briefly examine the relationship between the acoustic signature and the ocean currents.

EXPERIMENTAL DESIGN

The study was conducted aboard the NOAA ship Townsend Cromwell, July 1985 to January 1988, at the Southeast Hancock Seamount (lat. 29°48'N, long. 179°04'E), an open ocean seamount in the central North Pacific. Its summit depth is about 265 m; the bottom depth of the surrounding ocean is nearly 5 km. All times are reported as local standard time.

Observations of acoustic scattering were made with a 38 kHz Simrad[1] echo sounder (model EQ-38) operating with a pulse length of 0.3 ms and a time varied gain (TVG) of about 40 log(R) + 2αR [10]. A Raytheon-JRC chromoscope was configured to display the signal of the Simrad by assigning the echo voltage to one of several bins (1985, N = 12; 1988, N = 8) on the basis of signal strength. Each bin was represented by a unique color, which was displayed on a monitor as a function of depth and ship position. The composite chromoscope screen images were photographed with color slide film (35 mm) for later data analysis. Diel behavior of seamount-associated scattering layers was observed in 1985 by periodically running transects along an east to west line intersecting the center of the summit along lat. 29°48.0′N.

Relative biomass of the sonic scattering layer (SSL) at the Southeast Hancock Seamount was estimated from acoustic data collected in 1988 while the vessel ran at a nominal speed of 2.5 m/s along 6 km long transects over the summit and flanks and oriented at 45 degrees to one another. Transects began and ended about 1.9 km beyond the summit edge (transect end depths, ca. 700-1000 m). Identical instrument and camera settings were used during relative biomass assessment transects. The instrument settings on the chromoscope-echo sounder system were quantified by a Simrad echo probe, which provided a constant, continuous wave test signal to the input of the echo sounder receiver to determine the specific echo voltage level represented by each "color bin" for calibration purposes.

To determine relative estimates of biomass of sonic scatterers (which are proportional to the echo voltage squared) [11], the echo voltage level for each data cell was first calculated by visual "echo integration" of all colors comprising each chromoscope image. Data cells were constructed by dividing the transect into eight contiguous regions (each about 0.75 km long), which were subdivided into either five or seven depth strata of 50 m, each between depths of 10-260 m or 10-360 m over the summit and flanks, respectively. The relative cell area covered by each color was determined visually by projecting the 35 mm color slide image on a projector display screen overlaid with a grid of 2 mm squares. Heavy lines were drawn over the plastic grid to delineate each depth cell. About 60 grid squares were included in a cell; the reader made an assessment of the relative area that each of the eight colors occupied within a cell by determining the number of grid squares for each color. Each cell area was thus characterized by eight values corresponding to percentages of each color. The total echo voltage for each cell was calculated as the sum of each specific color voltage, after weighting each value by the relative cell area covered for each respective color. Before the total echo voltage for each cell was calculated, however, color-specific voltages were adjusted to represent voltage levels equivalent to those that would have resulted under a 20 log(R) + 2αR TVG function. This correction was necessary because, under a 20 log(R) + 2αR TVG function, the sum of the squared echo voltage over the depth of interest is proportional to the relative biomass of the SSL over the same depth range [10]. The 40 log(R) + $2\alpha R$ TVG function used in the Simrad (model EQ-38) echo sounder reaches a maximum at about the 150 m depth (R. Brede, Simrad Corp., pers. commun.); thus, raw echo voltage values beyond this depth needed to be adjusted to values that would have resulted if taken under a 20 log(R) + $2\alpha R$ TVG function over the full depth range.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

To adjust the echo voltages, first the TVG function of the instrument was quantified by recording voltage levels as a function of time (depth) for a given input test voltage level from the echo probe. From these values, the instrument TVG curve was constructed. For depths at which the TVG function of the instrument operated ($\leq$150 m), the differences between the observed voltage levels and the voltage levels subjected to a 20 log(R) + $2\alpha R$ function were used to calculate correction factors to correct observed voltages to values appropriate for relative biomass estimation (20 log(R) + $2\alpha R$). These corrections were then used to correct observed voltages from the SSL to values that would have been derived with a 20 log(R) + $2\alpha R$ TVG function. For depths beyond the operating range of the TVG function of the instrument, the observed voltage for each color was amplified with a 20 log(R) + $2\alpha R$ function.

Biological sampling to confirm acoustic targets used midwater trawls. A 1.8 m Isaacs-Kidd midwater trawl (IKMT) sampled the micronekton, a calibrated flowmeter estimated the volume of seawater filtered, and time-depth recorders registered the depth profile of each tow. Two larger midwater trawls were also used: The first was a Marinovich herring trawl with a mouth opening of 60 m^2 and body mesh of 19 mm; the second was a 264 rope wing trawl with a mouth opening of 400 m^2 and graduated mesh to as small as 100 mm. A Furuno net sonde system targeted specific components of the scattering layer to capture larger organisms not sampled by the IKMT.

Mean current velocity was estimated over the seamount summit using data collected from a vessel-mounted 150 kHz acoustic Doppler current profiler (ADCP) manufactured by RD Instruments. The ADCP data were collected with an 8 m pulse length and bin width and were initially averaged over 45 s intervals. Water velocity estimates relative to the vessel were referenced to absolute ship velocity estimates based on ADCP bottom tracking [12]. Usable data were collected and averaged between 40 and 210 m depths. The ADCP calibration runs similar to those conducted with other vessels [13] were conducted in 1988 to determine the transducer misalignment angle and amplitude bias [14]. Absolute ship velocities were determined with a NAVSTAR Global Positioning System (GPS) and by ADCP bottom tracking. The calibration coefficients were applied to ADCP velocity estimates.

The ADCP data from the summit center were collected while the vessel ran transects (described earlier) to estimate relative SSL abundance. Because all transects intersected at the center of the summit, we assumed velocity estimates averaged over 15- to 20-min intervals from the central portion of any transect profiled the same area. Velocity profiles from the central portions of the two transects immediately preceding the one presented in Figure 2 were averaged together with the latter transect to generate the estimate of mean current velocity.

RESULTS AND DISCUSSION

Acoustic observations on 12-13 July 1985 on the behavior of seamount-associated scattering layers showed a characteristic diel behavior (Fig. 1). The scatterers could often be distinguished acoustically during the day on the flanks of the seamount at about the 400 m depth. As dusk approached, the scatterers began moving upward, but the distribution of this movement was not uniform across the seamount summit (Fig. 1A). Just after sunset, the acoustic targets intensified and moved to shallower (ca. 50 m) water (Fig. 1B); the scattering layer later moved to deeper water and dispersed over a broader area around the seamount (Fig. 1C). The layer remained relatively stationary and uniform throughout the night but began dispersing in the early morning (Fig. 1D). In association with the increase in light intensity about 50 min before sunrise, some scatterers dispersed upwards, reaching shallower water (Fig. 1E). This was followed by consolidation of the layer, which moved rapidly downward as the sun rose above the horizon. Some scatterers remained in the water column above the seamount flanks later in the morning (Fig. 1F). No deep scattering layers in surrounding oceanic waters displayed this type of behavior.

Midwater trawl samples from the scattering layers in 1985-88 showed the sternoptychid fish Maurolicus muelleri and the mysid Gnathophausia longispina to be dominant components of the micronekton, with the sepiolid squid Iridoteuthis iris relatively common in the deeper portions of the scattering layer [5]. Oceanic micronekton, such as euphausiids and midwater fishes, were also present. Comparison tows taken in waters distant from the seamount lacked the three seamount-associated species but were characterized by greater abundance of certain open ocean taxa, such as the photichthyid fish Vinciguerria attenuata and V. nimbaria, and crustacean groups, such as euphausiids and caridean and penaeid shrimps [5].

Samples from large midwater trawls demonstrate the potentially high density of selected taxa and also the presence of larger fishes not sampled by the IKMT. In 1985, for example, a deployment of the Marinovich trawl in the scattering layer corresponding to Figure 1B took approximately 4400 M. muelleri in a short tow. This same species has been seen at densities as high as 147 metric tons/km^2 over seamounts in the South Atlantic [15]. One haul from the larger mesh rope trawl sampling a scattering layer in September 1986 produced 563 specimens of the gempylid fish Promethichthys prometheus (34.2-54.2 cm fork length). Based on these samples, the scattering layer may be much more dense locally than indicated by the smaller IKMT samples and may also be composed of organisms larger than micronekton.

Based on the acoustic data, relatively greater densities of scatterers were located on the southern side of the seamount at or slightly below summit depth when compared with the north summit region (Fig. 2). In addition, scatterers were relatively rare in water shallower than 50 m or in deep water to the north of the seamount. The mean current estimate during this period (2330-0150 h) demonstrates that the high relative biomass was on the downstream side of the seamount during this transect, suggesting the general morphology and location of the scattering layer over the seamount were probably functions of the current pattern at that time. However, the vertical component of the scattering distribution may be more a function of the swimming behavior of the organisms. These

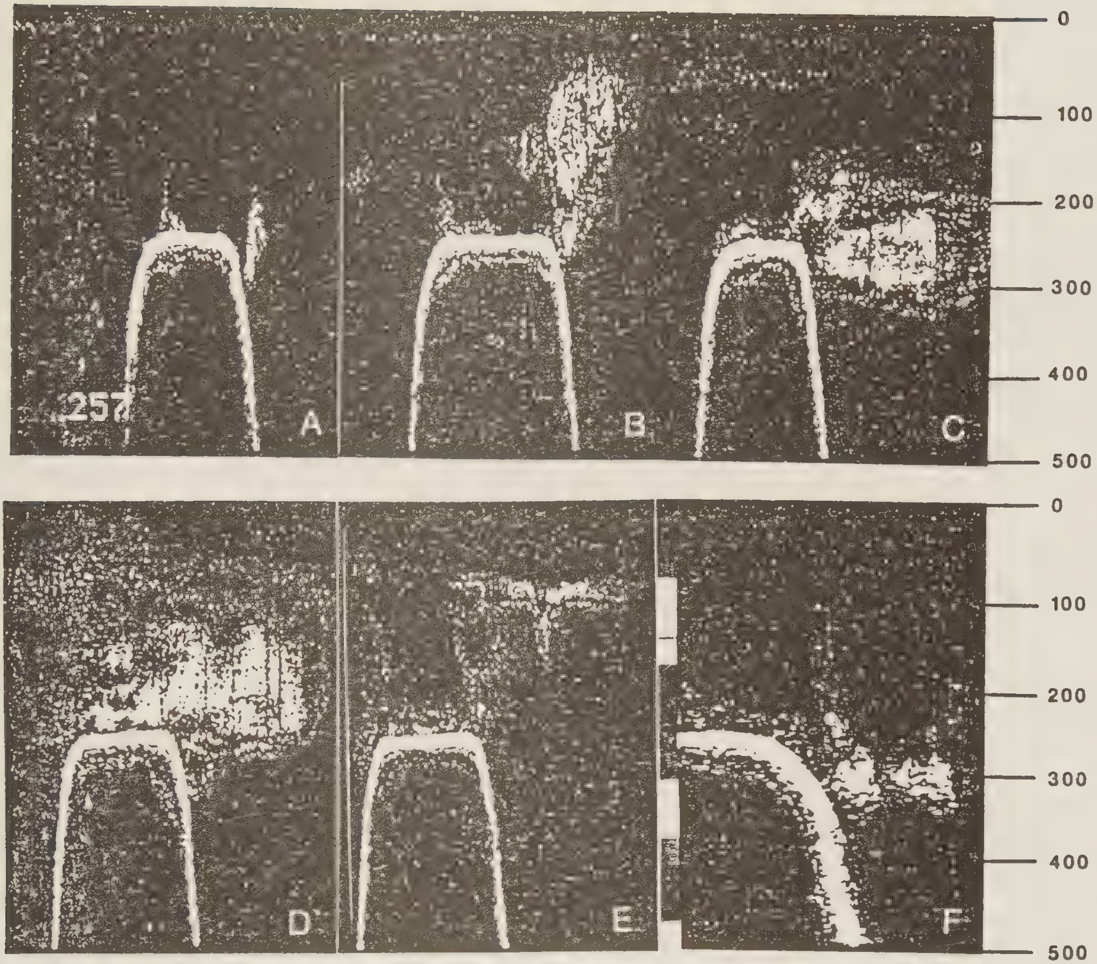

FIGURE 1. Acoustic transects over the Southeast Hancock Seamount on 12-13 July 1985 showing distribution of the scattering organisms over time. Depths are in meters. Each transect, from east to west (left to right), took approximately 25 min. The distance across the flat portion of the seamount is approximately 2.6 km. A. 1824 local standard time. The scattering organisms begin the initial ascent from the summit and western flank. Sunset was at 2003. B. 2015. The targets have moved to shallower water, and the scattering signal has intensified. C. 0027. The layer has dispersed slightly but at depths below 200 m (change near right side is due to inadvertent change in gain setting). D. 0355. Dispersion and some ascent is noted. E. 0514. The scattering layer consolidates in shallower water near sunrise at 0608. F. 0654. Large, discrete scattering targets remain below summit depth (horizontal scale differs on this figure).

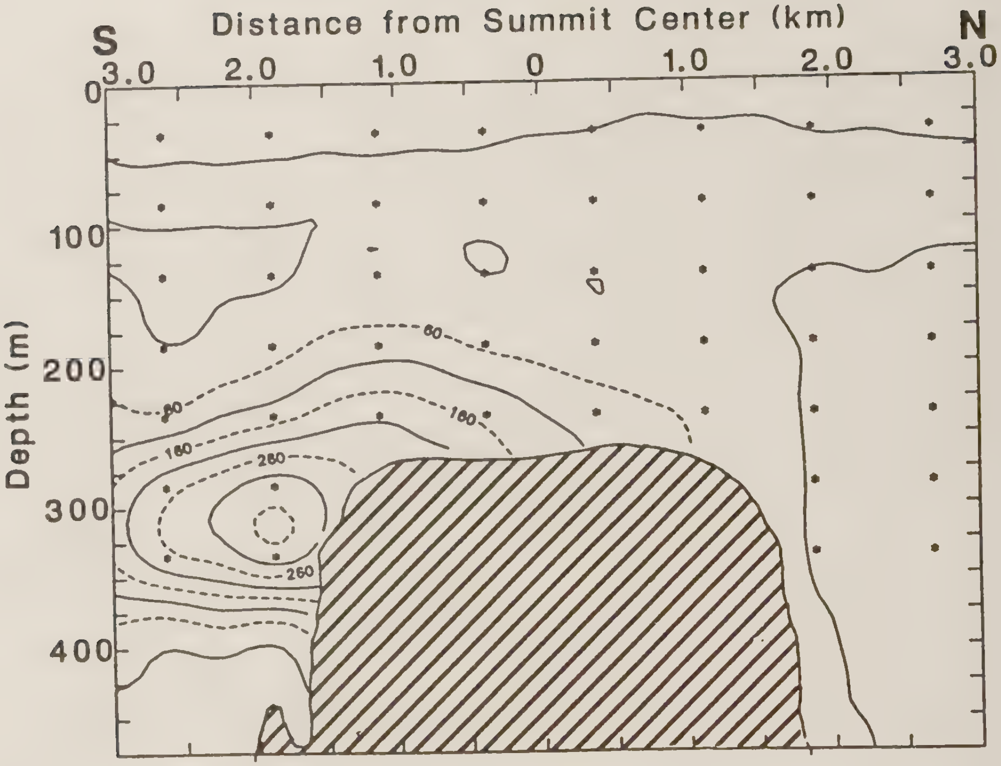

FIGURE 2. Acoustic section run from south to north (left to right) showing the contours of relative biomass of acoustic scatterers; the profile of the seamount is indicated by cross-hatching. This transect was made on 16 January 1988 at 0120 local standard time. Asterisks indicate the center of the 750 by 50 m bins where relative biomass was estimated and used as data points for contouring. Contour values represent an arbitrary scale of relative density units (see text for explanation). Estimated current velocity during this period was to the south (185°) at a speed of 17 cm/s.

results suggest that current speed during the transects in 1985 (when current was not measured) was probably from east to west (Fig. 1 B, C, D). Further research is needed to discern the relationship between the form of the acoustic scattering layer and the current speed and direction.

Variability of acoustic scattering due to biological activity around topography may interfere with ADCP-derived current estimates. For example, the high relative densities of organisms comprising the SSL associated with the seamount summit (Figs. 1, 2) may potentially bias estimates of velocity based on ADCP data. When ship velocity estimates are derived from ADCP instrument acoustic returns from the summit itself (i.e. bottom tracking [12]), it is critical that the instrument can distinguish between echoes reflected from the substrate versus those from the SSL. If the instrument is unable to resolve bottom and SSL echo signals, absolute velocity estimates will be in error. Although RDI instrument settings may be adjusted to optimize criteria used in identifying signals reflected from the substrate, we have found that variable, but high, densities of SSL at the Southeast Hancock Seamount have required careful post-cruise editing of the data to remove SSL echo signals that had been incorrectly labeled as valid bottom signals. Using factory default settings during the transect presented in Figure 2, for example, the instrument identified a false bottom at 275-350 m depths while approaching the south side of the summit (bottom depth, >500 m) over a dense SSL, whereas no false bottom was detected north of the summit, an area characterized by relatively few scatterers. Additional work is being conducted to determine suitable settings to optimize performance of the instrument when bottom tracking under conditions when dense SSLs occur. In the presence of such scattering layers, however, caution must be exercised in the interpretation of ADCP measurements. Vertical velocities (Fig. 1 A, B) on the order of 16 cm/s can be expected for vertically migrating micronekton [16]. The extent of directed horizontal movements within the seamount scattering layers is unknown, but similar swimming speeds could bias acoustically measured currents since the ADCP measures the speed of the scatterers, not the water.

CONCLUSIONS

The behavior of micronekton and nekton near the Southeast Hancock Seamount has a characteristic diel pattern that differs from scattering layers in surrounding oceanic waters. From night to night, the horizontal distribution of scatterers appears to be modified by the direction and magnitude of impinging currents. More detailed study with multibeam acoustic technology, net sampling, and time series of current measurements will be necessary to identify the behavior of individual species comprising these SSL.

REFERENCES

[1] RODEN, G.I., 1987: Effect of seamounts and seamount chains on ocean circulation and thermohaline structure, pp. 335-354. *In*: B.H. Keating, P. Fryer, R. Batiza and G.W. Boehlert, eds., Seamounts, islands, and atolls. Geophys.Monogr. *43*.

[2] BOEHLERT, G.W. and GENIN, A., 1987: A review of the effects of seamounts on biological processes, pp. 319-334. *In*: B.H. Keating, P. Fryer, R. Batiza and G.W. Boehlert, eds., Seamounts, islands, and atolls. Geophys.Monogr. *43*.

[3] HARGREAVES, P.M., 1975: Some observations on the relative abundance of biological sound scatterers in the northeastern Atlantic Ocean, with particular reference to apparent fish shoals, Mar.Biol. *29*. 71-87.

[4] BOEHLERT, G.W., 1988: Seamount acoustic scattering. Nocturnal emissions or organismal activities?, EOS, Trans.Am.Geophys. Union *69*, 1619, 1628.

[5] BOEHLERT, G.W., 1988: Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems, Proc. 1st Pacific Symp.Mar.Sci., Nakhodka, U.S.S.R., GeoJournal *16*, 45-52.

[6] DARNITSKY, V.B., BOLDYREV, V.L. and VOLKOV, A.F., 1984: Environmental conditions and some ecological characteristics of fishes from the central North Pacific seamounts, pp. 64-77. *In* P.A. Moiseev, ed., Proc., Conditions of Formation of Commercial Fish Concentrations, Ministry of Fisheries, Moscow, U.S.S.R., All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO).

[7] ISAACS, J.D. and SCHWARTZLOSE, R.A., 1965: Migrant sound scatterers: Interactions with the sea floor, Science *150*, 1810-1813.

[8] GENIN, A., HAURY, L. and GREENBLATT, P., 1988: Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness, Deep-Sea Res. *35*, 151-175.

[9] LARINA, N.I., 1976: Seamounts of the Pacific Ocean, Oceanology *15*, 62-66.

[10] BURCZYNSKI, J., 1982: Introduction to the use of sonar systems for estimating fish biomass, FAO Fish.Tech.Pap. *191* (Rev. 1), 89 pp.

[11] JOHANNESSON, K.A. and MITSON, R.B., 1983: Fisheries acoustics. A practical manual for aquatic biomass estimation, FAO Fish.Tech.Pap. *240*, 249 pp.

[12] R.D. INSTRUMENTS, 1988: Acoustic Doppler current profilers principles of operation: A practical primer, R.D. Instruments, San Diego, California, 39 pp.

[13] POLLARD, R. and READ, J., In press: A method for calibrating ship-mounted acoustic Doppler profilers, and the limitations of gyro compasses. J.Atmos. Oceanic Tech.

[14] WILSON, C.D., Unpublished MS: Instrument calibration of a vessel-mounted acoustic Doppler current profiler (ADCP) and comparison of ADCP current estimates based on GPS versus radar navigation.

[15] KALINOWSKI, J. and LINKOWSKI, T.B., 1983: Hydroacoustic observations on Maurolicus muelleri (Sternoptychidae) over R.S.A. and Discovery Seamounts (South Atlantic). International Council for the Exploration of the Sea, Pelagic Fish Committee, CM-1983/H:16, 20 pp.

[16] BODEN, B.P. and KAMPA, E.M., 1967: The influence of natural light on the vertical migrations of an animal community in the sea. Symp.Zool.Soc. Lond. *19*, 15-26.

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THE EFFECTS OF DIFFERENT OTOLITH AGEING TECHNIQUES ON ESTIMATES OF GROWTH AND MORTALITY FOR THE SPLITNOSE ROCKFISH, *SEBASTES DIPLOPROA,* AND CANARY ROCKFISH, *S. PINNIGER*

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Different ageing techniques affect not only the estimates of length at age but also estimates of population growth and mortality rates. This study considers these effects for the splitnose rockfish, *Sebastes diploproa,* and canary rockfish, *S. pinniger,* based on ages determined from the surfaces and sections of otoliths collected during a trawl survey off the west coast of North America in 1980. Estimates of growth based on surface rather than section ages were nearly identical for *S. diploproa* but were higher for *S. pinniger;* slightly different whole otolith ageing techniques are suspected of producing these interspecific differences. For both species, however, estimates of mortality were reduced by more than half when section rather than surface ages were used.

INTRODUCTION

Ages of fish are needed to estimate two vital parameters of exploited fish populations, namely growth and mortality rates. Many fish species typically are aged by interpreting rings on the otolith, as is the case for rockfishes (*Sebastes*) for which the otolith is the preferred ageing structure (Six and Horton 1977, Chilton and Beamish 1982). Various techniques have been developed to facilitate the detection and the interpretation of otolith patterns used in age determination (Chilton and Beamish 1982). Two methods to determine ages are counting the number of rings or annuli viewed on the exterior of the whole otolith (surface ages) or on a lateral cross section of the otolith (section ages). Section ages are often greater than surface ages for older specimens of many long-lived, slow-growing species (Beamish 1979a, 1979b, Boehlert and Yoklavich 1984), and recent evidence demonstrates that the section ages represent the true ages of fish (Bennett et al. 1982, Leaman and Nagtegaal 1987 Campana et al. in press).

Because present evidence supports the validity of section ages for older fish, important biological and management implications could result if many demersal fish stocks are underaged due to the more common surface ageing

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technique. Archibald et al. (1981) found that estimates of instantaneous mortality (*Z*) were reduced by as much as 50% when the otolith sections were used to age 10 species of rockfishes. Even for fishes that are not long lived, age length data without older fish affect the estimation of von Bertalanffy growth parameters (Hirschhorn 1974). Because population size, growth, and mortality are the basic data required for most production modeling, systematic bias in age determination may lead to serious errors in determining stock production estimates (Le Cren 1974). In the present study, we determine whether significant differences in the estimates of growth and mortality rates are affected by the method of otolith age determination for two species of *Sebastes*—the splitnose rockfish, *S. diploproa,* and canary rockfish, *S. pinniger.*

MATERIALS AND METHODS

Otoliths from *S. diploproa* and *S. pinniger* were collected during a 1980 trawl survey conducted off the west coast of North America (lat 36° 49′ to 50° 00′N). Gear, sampling design, and catch processing generally followed the procedures in Dark et al. (1983). Several differences in the collection and care of otoliths have been described by Boehlert and Yoklavich (1984). Otoliths used in the present study were initially collected for other work; therefore, fish comprising the age subsample were systematically chosen until a predetermined number for each size class was attained. When mortality rates were estimated in the present study, the original age subsample was applied to a simple random sample of length-frequency data to remove any potential sampling bias (Dark 1975) which may have been introduced during sample collection.

The length-frequency data were chosen for each species in the following manner. For *S. pinniger,* the limited length-frequency data from the 1980 survey were combined with length-frequency data collected in 1980 by the Washington Department of Fisheries and the Oregon Department of Fish and Wildlife. For *S. diploproa,* the length-frequency sample was restricted to fish from lat 40° 26′ to 48° 47′ N, where 76% of the fish in the age sample were collected. This was done because Boehlert and Kappenman (1980) detected increases in growth rate with latitude for *S. diploproa* when specimens were compared from this and two other geographic regions (i.e., lat 34°–37°, 37°–40°, 40°–48° N). Thus, all *S. diploproa* otoliths were analyzed as a single stock, even though 24% were collected south of 40° N, in order that the effects of using surface versus section ages could be evaluated with as large an age sample as possible. Resulting growth curves would most likely represent fish from the northernmost strata (40°–48° N) described by Boehlert and Kappenman (1980).

Ageing

Ages were determined from the same whole and sectioned left sagittal otolith of *S. diploproa* and *S. pinniger* by one of three readers from the same laboratory. The variability in ageing the otolith data set within and between readers is presented in Boehlert and Yoklavich (1984). Surface ages for both species were derived from whole otoliths by the method of Boehlert and Yoklavich (1984). The otolith was read from the focus to the dorsal edge or, in the case of older individuals, from the focus to the posterodorsal region (Figure 1A, 1B). Otoliths from many older specimens, particularly *S. diploproa,* possess posterior projections. Pairs of translucent and opaque bands in these regions were included in the counts for *S. diploproa* but not for *S. pinniger;* methodology for the latter species follows the general technique in Six and Horton (1977)

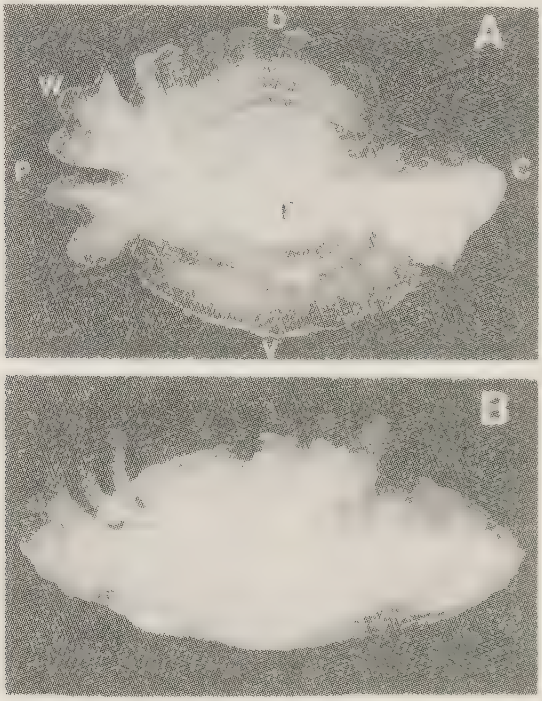

FIGURE 1. External surface of the whole otolith from (A) a 32 cm fork length (FL) female *Sebastes diploproa* with a surface age of 22 years and a section age of 25 years, and (B) a 52 cm FL male *S. pinniger* with a surface age of 18 years and a section age of 19 years. (C) anterior, (D) dorsal, (F) focus, (P) posterior, (V) ventral, (W) posterior projection.

Dorsoventral otolith sections (0.4 mm thick; Figure 2) were obtained with a double-bladed diamond saw; each section was mounted on a microscope slide and polished to remove surface artifacts (Nichy 1977, Boehlert 1985). The otolith section was read (30X or 100X) from the focus to the dorsal edge. For older individuals, the reader began counting toward the dorsal tip, then followed a distinct ring from the dorsal region of the section into the internal dorsal quadrant and continued counting towards the section edge (Figure 2).

In many species of rockfishes, surface and section ages tend to agree for younger individuals (Beamish 1979b, Shaw and Archibald 1981, Boehlert and Yoklavich 1984). For example, G. Boehlert and M. Yoklavich (unpub. data) systematically subsampled every fourth otolith pair from *S. diploproa* and every third otolith pair from *S. pinniger* used in this study and found mean differences between surface and section ages of ≤ 2 years for *S. diploproa* females aged ≤ 12 and males ≤ 17 years and *S. pinniger* females ≤ 7 and males ≤ 8 years. For this reason, we assigned a section age equal to the surface age for all remaining otoliths with surface ages less than or equal to the values listed above. Thus, an otolith from an *S. pinniger* male with a surface age of 6 years was given a section age of 6 years if the otolith had not been included earlier in the subsample. This procedure allowed an increased sample size.

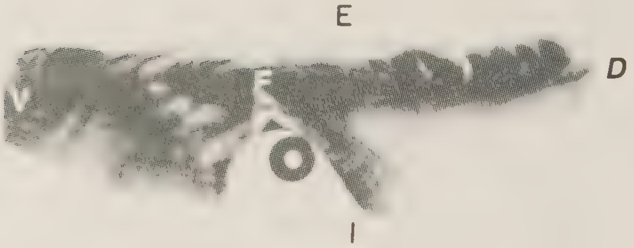

FIGURE 2. Dorsoventral cross section of the left otolith from a 31 cm fork length (FL) *Sebastes diploproa* with a surface age of 28 years and a section age of 39 years. (D) dorsal, (F) focus, (E) external surface, (I) internal surface, (V) ventral. Surface ages were determined by counting rings on the external side of the otolith from the focus towards the dorsal edge.

Mortality and Growth Rates

Total instantaneous mortality rates (Z) were estimated by calculating the slope of the descending right side of the age-frequency distribution (catch curve) by simple linear regression (Ricker 1975). Total instantaneous mortality rates were compared by using an F-test (Neter and Wasserman 1974).

Individual length at age data were fit to the von Bertalanffy growth model (Ricker 1975) by a nonlinear regression routine (Dixon 1981). Von Bertalanffy growth curves were compared by using the chi-square test for homogeneity of individual parameters (Rao 1973) and by the method developed by Gallucci and Quinn (1979) in which the von Bertalanffy growth function is reparameterized with the introduction of a new parameter (ω). Results of all statistical tests were considered significant at $P \leq 0.05$.

RESULTS

Sebastes pinniger

Otoliths were collected from a total of 363 female and 516 male *S. pinniger* specimens between latitudes 43° 11′ and 49° 16′ N. Females had maximum surface ages to 22 years and section ages to 34 years (Table 1). Differences between the two methods were greater for males; maximum surface and section ages were 25 and 60 years, respectively (Table 1).

Fitted growth curves for males based on each ageing method are more similar than growth curves for females. Estimates of L_∞ for both sexes based on surface ages significantly exceeded those based on section ages (by nearly 6 cm fork length (FL) for females and 4 cm FL for males, Figure 3). The difference in growth estimates between treatments apparently occurs beyond the region of the curve where statistical tests on ω are most powerful (Gulland 1983).

TABLE 1. **Mean Fork Lengths at Age (FL in Centimeters) and Standard Deviation (SD) for Female and Male *Sebastes pinniger* Based on Surface and Section Ages. *N* Indicates the Number of Otoliths.**

Age	*Surface*			*Section*		
	N	*FL*	*SD*	*N*	*FL*	*SD*
			Females			
1	—	—	—	—	—	—
2	4	15.50	0.58	3	15.67	0.58
3	—	—	—	1	15.00	—
4	3	30.00	4.36	3	30.00	4.36
5	4	31.75	0.50	2	32.00	—
6	11	37.27	3.55	8	36.38	3.50
7	6	37.67	1.86	5	36.80	3.70
8	18	41.28	2.70	9	41.00	7.63
9	13	44.08	4.52	16	43.50	3.20
10	18	46.11	3.43	20	46.10	3.65
11	37	49.27	2.91	28	46.71	4.47
12	64	49.92	2.69	50	49.50	3.70
13	57	52.23	2.49	47	50.64	3.59
14	38	53.97	2.83	34	52.53	2.26
15	33	54.48	2.58	18	52.22	3.14
16	23	55.52	2.13	21	53.90	3.06
17	14	56.00	1.84	16	54.06	2.64
18	15	57.00	1.60	13	55.46	2.96
19	2	59.50	2.12	15	54.80	2.51
20	2	61.50	3.54	11	55.00	1.73
21	—	—	—	6	53.83	2.64
22	1	59.00	—	4	54.75	1.71
23	—	—	—	8	56.38	2.39
24	—	—	—	5	57.20	2.49
25	—	—	—	5	56.60	2.19
26	—	—	—	5	57.40	6.07
27	—	—	—	4	57.00	4.83
28	—	—	—	1	50.00	—
29	—	—	—	3	58.33	1.15
30	—	—	—	1	58.00	—
31	—	—	—	—	—	—
32	—	—	—	—	—	—
33	—	—	—	—	—	—
34	—	—	—	1	50.00	—
			Males			
1	—	—	—	—	—	—
2	3	16.00	1.73	2	15.50	2.12
3	5	21.80	1.30	4	20.25	2.50
4	3	25.00	3.61	4	24.25	3.30
5	4	35.25	4.92	3	33.00	8.72
6	3	35.33	1.53	6	34.17	3.31
7	20	38.70	3.63	13	39.31	3.86
8	24	40.42	2.47	22	40.36	2.61
9	18	43.61	3.45	9	43.78	3.03
10	29	45.24	2.89	18	43.06	4.08
11	42	47.00	2.85	20	45.05	3.75
12	70	48.49	1.85	35	47.09	2.73
13	69	49.59	2.02	28	47.79	2.77
14	55	50.22	1.90	22	47.45	3.69
15	47	51.55	1.77	23	47.83	2.37
16	52	51.79	2.05	13	50.46	2.26
17	25	52.84	1.65	23	49.13	1.89
18	24	53.46	1.82	24	50.71	1.90
19	9	53.33	1.32	27	49.89	1.97
20	6	53.67	2.25	27	50.48	2.59
21	3	53.33	0.58	27	51.33	2.11
22	4	54.25	0.96	22	50.32	2.06
23	—	—	—	12	51.50	1.83
24	—	—	—	12	50.42	1.83
25	1	57.00	—	12	50.58	3.68

(Continued)

TABLE 1.—Continued

26	—	—	—	14	52.07	2.23
27	—	—	—	8	52.50	2.14
28	—	—	—	7	52.14	2.34
29	—	—	—	2	51.00	1.41
30	—	—	—	5	52.60	1.82
31	—	—	—	10	52.30	2.63
32	—	—	—	3	51.67	0.58
33	—	—	—	8	52.50	1.85
34	—	—	—	3	54.00	1.00
35	—	—	—	6	52.83	1.17
36	—	—	—	3	54.33	4.62
37	—	—	—	2	52.50	2.12
38	—	—	—	10	52.80	1.99
39	—	—	—	1	52.00	—
40	—	—	—	6	52.67	1.86
41	—	—	—	2	54.00	1.41
42	—	—	—	2	53.50	0.71
43	—	—	—	1	53.00	—
44	—	—	—	1	52.00	—
45	—	—	—	4	53.25	1.89
46	—	—	—	1	50.00	—
47	—	—	—	1	48.00	—
48	—	—	—	1	52.00	—
49	—	—	—	—	—	—
50	—	—	—	2	52.00	1.41
51	—	—	—	—	—	—
52	—	—	—	1	53.00	—
53	—	—	—	1	53.00	—
54	—	—	—	—	—	—
55	—	—	—	—	—	—
56	—	—	—	1	56.00	—
57	—	—	—	—	—	—
58	—	—	—	—	—	—
59	—	—	—	1	55.00	—
60	—	—	—	1	56.00	—

Catch curves constructed from surface and section ages of *S. pinniger* clearly differed (Figure 4). Regardless of the ageing technique used, however, both sexes were fully recruited to the fishery by age 12. Estimates of *Z* derived from surface and section ages significantly differed for both sexes: *Z* values estimated from section ages were 61% less for females and 78% less for males than those calculated from surface ages (Table 2).

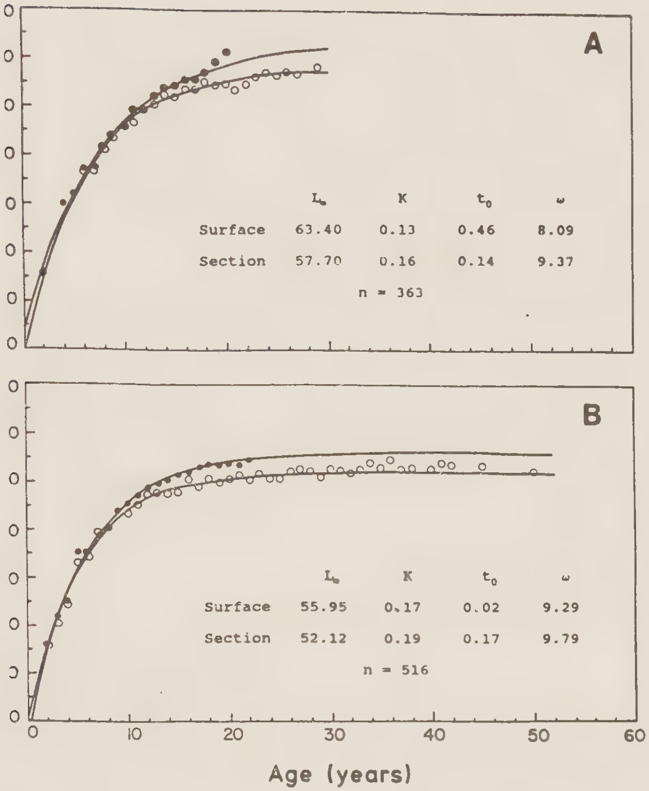

FIGURE 3. Fitted von Bertalanffy growth curves, parameter estimates (see text for explanation), and mean lengths at age based on surface (closed circles) and section ages (open circles) of otoliths from (A) female and (B) male *Sebastes pinniger.* Points representing single individuals are not shown. *N* indicates sample size.

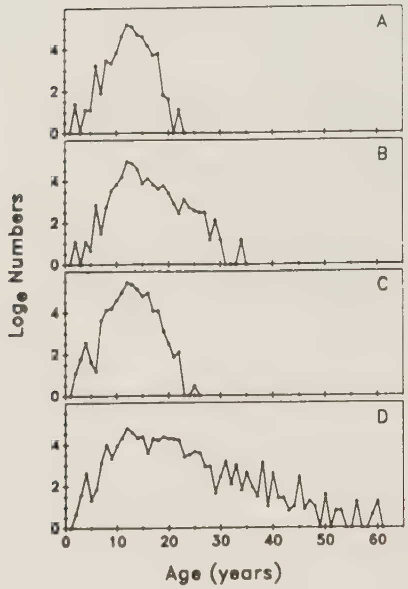

FIGURE 4. Catch curves based on (A, C) surface and (B, D) section ages of otoliths from (A, B) female and (C, D) male *Sebastes pinniger.*

Sebastes diploproa

Otoliths from 1,131 female and 922 male *S. diploproa* were collected between lat 36° 49′ and 48° 47′ N. Both sexes of *S. diploproa* reached much greater ages than those attained by *S. pinniger.* Female *S. diploproa* attained ages similar to males and had surface ages to 55 years and section ages to 81 years compared with 46 and 84 years, respectively, for males (Table 3). Growth curves of either sex based on surface and section ages were essentially identical, and parameter estimates and ω were not significantly different (Figure 5).

Catch curves constructed from surface and section ages of *S. diploproa* clearly differed (Figure 6). In all cases, particularly among females, substantial variation occurred between year classes, with a succession of weak year classes between ages 10 and 20. Therefore, Z was determined for fish older than 21 years. As with *S. pinniger,* significant differences were found between estimates of Z derived from surface and section ages for both sexes; estimates based on section ages were 55% less for females and 76% less for males than those based on surface ages (Table 2).

TABLE 2. Estimates of Total Instantaneous Mortality (*Z*) for *Sebastes pinniger* and *S. diploproa*. Range Indicates Ages Over Which *Z* Was Determined.

Sex	*Surface*		*Section*	
	Z	*Range*	*Z*	*Range*
		Sebastes pinniger		
Female	0.452	12–22	0.178	12–34
Male	0.405	12–25	0.089	12–60
		S. diploproa		
Female	0.109	25–48	0.049	22–71
Male	0.130	23–40	0.031	26–75

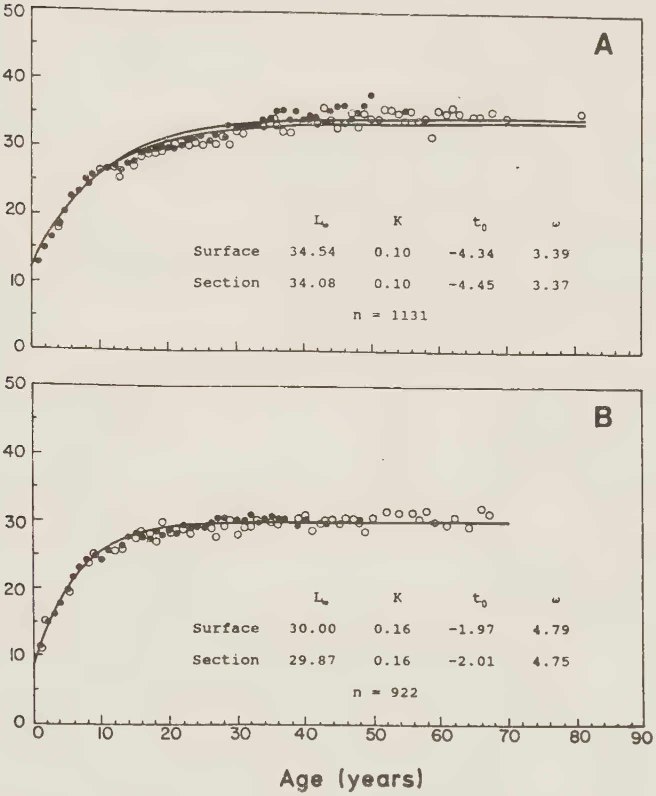

FIGURE 5. Fitted von Bertalanffy growth curves, parameter estimates (see text for explanation), and mean lengths at age based on surface (closed circles) and section ages (open circles) of otoliths from (A) female and (B) male *Sebastes diploproa*. Points representing single individuals are not shown. *N* indicates sample size.

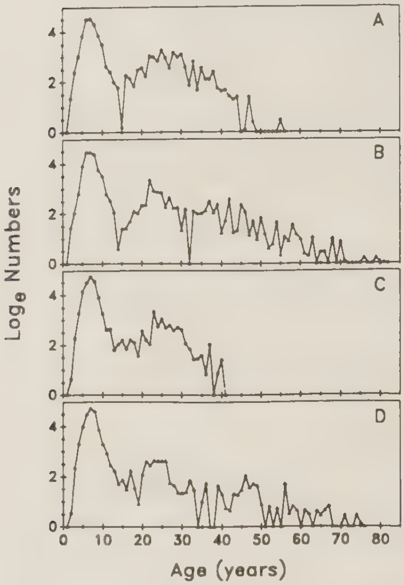

FIGURE 6. Catch curves based on (A, C) surface and (B, D) section ages of otoliths from (A, B) female and (C, D) male *Sebastes diploproa.*

DISCUSSION

Differences in Growth

The effects of changing the methodology of fish age determination can vary from a minor error to major differences. Estimates of maximum age in the genus *Sebastes* have changed markedly in recent years (Beamish 1979b; Bennett et al. 1982; Leaman and Nagtegaal 1987); thus, one would expect similarly remarkable differences in estimates of growth within a species. For *S. pinniger,* estimates of the L_∞ were significantly lower when section rather than surface ages were used although the increase in the growth completion rate (von Bertalanffy's *k*) for both sexes (Figure 3) was not significant. Therefore, when surface ages are used, errors in ageing incorrectly place older, larger individuals into younger age groups, thus inflating their mean lengths at age (Wilson 1985). This results in lower mean lengths at age for many of these section age groups relative to surface age groups, and a corresponding decrease in L_∞ based on section ages.

Another explanation to account for the differences between growth curves constructed from surface and section ages in *S. pinniger* is that a curve fitting problem occurs, particularly for females. Thus, L_∞ may be overestimated when data are available for only the ascending limb of the von Bertalanffy growth function (Knight 1968, Gallucci and Quinn 1979, Vaughan and Kanciruk 1982). Note that the estimate of L_∞ is typically greater than the maximum observed length in our study (Table 1, Figure 3). Because surface ages have a lower range than section ages and are more concentrated on the ascending limb of the growth curve, they may fail to adequately estimate the upper portion of the curve, which represents $L\infty$. For example, the large differences between estimates of $L\infty$ for female *S. pinniger* may occur because their surface ages are more concentrated on the ascending portion of the curve than are those of males (Table 1). This situation is analogous to fitting growth curves with incomplete representation of the range of ages (Hirschhorn 1974).

Unexpected results of our study were the similarities in estimated growth parameters for *S. diploproa* based upon section and surface ages (Figure 5) despite the much higher maximum section ages (Table 3). This difference from *S. pinniger* is likely due to our surface ageing methodology. We suggest that the surface ageing technique for *S. diploproa* has changed over several years to provide older age estimates. Boehlert (1980), for example, used surface ages and observed only 0.5% of all specimens in excess of 25 years of age compared with 18.9% in the present study. Earlier surface ages for *S. diploproa* were assigned without rolling or tilting the otoliths, thus preventing the enumeration of additional annuli on the posterior "winglike" projections (Figure 1A). More recently, annuli located on posterior projection (present in older individuals of many species of *Sebastes)* have been included in surface age counts in order that surface ages more closely represent section ages (Chilton and Beamish 1982, Boehlert and Yoklavich 1984). In the present study, surface ages for *S. pinniger* were assigned using standard criteria for this species (Six and Horton 1977) without including these counts (which are typically less well developed on otoliths of *S. pinniger)*; the counts were included in assigning surface ages to *S. diploproa*. Thus, while maximum ages increased, counts including the posterior projection resulted in surface ages closer to section ages and minimized the higher mean length estimates for ages on the ascending arm of the growth curve as seen in the surface ages of *S. pinniger* (Figures 3, 5). Had the age estimates from Boehlert (1980) or the "other agency" readers in Boehlert and Yoklavich (1984) been used, it is likely that differences in growth parameters similar to those for *S. pinniger* would have been observed for *S. diploproa*.

TABLE 3. Mean Fork Lengths at Age (FL in Centimeters) and Standard Deviation (SD) for Female and Male *Sebastes diploproa* Based on Surface and Section Ages. *N* Indicates the Number of Otoliths.

	Surface			*Section*		
Age	*N*	*FL*	*SD*	*N*	*FL*	*SD*
			Females			
1	8	13.00	1.31	7	12.86	1.35
2	12	14.83	1.53	14	14.93	1.54
3	24	16.54	1.38	18	16.50	1.54
4	36	18.47	2.09	32	17.72	2.04
5	68	20.40	2.31	76	20.38	2.23
6	119	22.59	2.02	117	22.60	2.03
7	125	23.22	2.02	117	23.15	2.04
8	119	24.97	2.21	130	24.97	2.14
9	82	25.71	1.92	75	25.73	2.05
10	61	26.48	2.47	60	26.30	2.68
11	25	26.56	1.45	30	26.63	1.43
12	20	27.15	3.28	21	27.00	2.66
13	13	26.46	2.50	12	25.50	3.53
14	8	27.50	1.69	4	27.50	1.73
15	2	28.00	1.41	6	27.17	2.64
16	11	29.36	2.42	5	28.60	2.07
17	10	29.30	1.77	7	29.14	1.57
18	7	29.71	1.60	11	29.45	0.93

(Continued)

TABLE 3—Continued

19	13	30.15	1.68	7	29.57	2.15
20	15	30.13	1.06	11	30.36	1.80
21	10	30.00	2.45	11	30.36	1.75
22	21	30.71	1.55	27	30.81	1.49
23	18	31.33	1.88	19	30.37	1.67
24	17	31.53	2.37	15	30.80	0.94
25	25	31.80	1.91	17	30.59	1.37
26	18	31.33	1.97	9	31.22	1.99
27	14	32.21	2.46	14	30.79	2.12
28	23	32.22	2.19	9	31.89	2.15
29	20	33.30	1.81	9	30.56	2.01
30	21	33.19	1.57	3	32.67	1.53
31	14	33.07	2.40	8	32.25	1.75
32	9	33.33	3.16	1	37.00	—
33	17	33.47	2.15	9	33.44	2.30
34	7	34.29	2.56	7	33.43	1.72
35	17	34.53	2.53	9	34.22	2.17
36	15	35.53	1.60	9	33.56	1.51
37	12	35.58	1.73	12	32.58	1.73
38	15	34.47	2.50	7	32.57	1.90
39	10	35.50	1.90	13	33.77	2.86
40	6	34.33	1.86	4	34.25	2.36
41	8	35.00	2.14	8	34.38	2.39
42	5	34.60	2.51	5	33.87	2.00
43	4	34.00	1.41	7	36.00	1.15
44	7	35.57	1.13	4	34.50	1.29
45	2	36.50	0.71	11	33.09	1.97
46	4	36.50	1.00	11	35.33	3.30
47	5	34.80	1.64	6	33.29	2.73
48	2	35.50	0.71	7	33.29	2.43
49	2	36.50	0.71	3	35.33	0.58
50	2	38.00	1.41	10	34.50	2.68
51	—	—	—	4	34.50	1.91
52	—	—	—	4	36.00	1.41
53	—	—	—	5	36.00	1.22
54	—	—	—	8	35.37	2.45
55	3	36.00	1.00	2	34.50	2.12
56	—	—	—	6	35.83	1.94
57	—	—	—	4	34.25	3.10
58	—	—	—	6	34.67	2.34
59	—	—	—	3	32.00	2.65
60	—	—	—	5	35.80	1.92
61	—	—	—	2	35.50	0.71
62	—	—	—	3	36.33	2.08
63	—	—	—	4	35.50	1.29
64	—	—	—	—	—	—
65	—	—	—	2	35.50	1.41
66	—	—	—	2	35.00	1.41
67	—	—	—	—	—	—
68	—	—	—	4	35.75	1.71
69	—	—	—	1	38.00	—
70	—	—	—	3	34.67	2.08
71	—	—	—	1	35.00	—
72	—	—	—	1	30.00	—
73	—	—	—	—	—	—
74	—	—	—	—	—	—
75	—	—	—	1	39.00	—
76	—	—	—	1	34.00	—
77	—	—	—	—	—	—
78	—	—	—	1	36.00	—
79	—	—	—	1	34.00	—
80	—	—	—	1	36.00	—
81	—	—	—	2	35.50	3.54
				Males		
1	12	11.33	1.61	11	11.09	1.45
2	8	14.87	0.99	6	15.00	1.10

(Continued)

TABLE 3—Continued

	Surface			*Section*		
Age	*N*	*FL*	*SD*	*N*	*FL*	*SD*
3	27	16.15	2.16	27	16.48	2.08
4	47	17.70	1.92	48	17.63	2.05
5	86	19.98	2.02	79	19.77	2.25
6	100	21.87	1.86	101	21.71	1.96
7	128	23.23	1.82	124	23.16	1.83
8	114	24.32	1.91	119	24.12	2.11
9	62	24.69	2.05	61	24.90	1.79
10	30	24.23	2 16	32	24.28	2.25
11	15	25.53	3.20	21	25.52	3.12
12	16	25.81	1.83	14	25.57	1.70
13	7	26.43	1.72	11	25.82	2.96
14	8	27.63	2.07	6	27.67	2.42
15	9	28.22	0.83	8	27.63	1.30
16	7	27.57	1.27	5	28.40	1.67
17	11	27.64	1.43	10	28.50	1.27
18	9	28.56	1.51	6	27.17	1.17
19	5	28.00	1.22	3	29.67	1.15
20	13	28.92	1.12	9	28.67	1.41
21	9	28.44	1.67	14	28.64	1.08
22	9	29.56	2.13	12	28.92	1.24
23	29	28.93	2.20	14	28.32	1.50
24	16	29.44	1.71	13	29.31	1.18
25	20	29.15	1.31	14	29.43	1.40
26	15	29.73	1.10	15	29.13	0.99
27	17	30.41	1.84	6	27.67	3.88
28	13	30.46	1.39	6	29.50	0.84
29	16	29.94	1.18	5	30.20	1.10
30	16	30.19	2.48	4	28.25	2.50
31	9	30.11	1.90	4	29.25	0.96
32	6	31.00	0.89	6	29.33	1.75
33	4	29.75	2.22	5	30.00	0.71
34	5	30.40	0.55	1	30.00	—
35	5	30.80	0.84	2	30.00	2.83
36	3	30.33	1.15	6	29.83	0.98
37	7	30.43	1.27	1	30.00	—
38	1	30.00	—	1	26.00	—
39	2	29.50	3.54	4	30.25	2.63
40	4	30.50	1.29	4	30.75	1.71
41	1	31.00	—	2	28.50	0.71
42	—	—	—	2	29.50	2.12
43	—	—	—	3	30.00	2.00
44	—	—	—	4	30.25	0.50
45	—	—	—	5	29.80	0.84
46	1	31.00	—	8	30.50	1.51
47	—	—	—	5	30.20	1.92
48	—	—	—	6	29.83	2.86
49	—	—	—	6	28.67	1.63
50	—	—	—	2	30.50	2.12
51	—	—	—	1	31.00	—
52	—	—	—	2	31.50	0.71
53	—	—	—	1	30.00	—
54	—	—	—	3	31.33	2.52
55	—	—	—	1	30.00	—
56	—	—	—	6	31.50	0.84
57	—	—	—	2	30.50	0.71
58	—	—	—	2	31.50	0.71
59	—	—	—	2	30.00	—
60	—	—	—	1	30.00	—
61	—	—	—	2	29.50	2.12
62	—	—	—	2	30.50	0.71
63	—	—	—	1	29.00	—
64	—	—	—	2	29.50	0.71
65	—	—	—	1	32.00	—

(Continued)

TABLE 3—Continued

66	—	—	—	3	32.00	1.73
67	—	—	—	2	31.50	0.71
68	—	—	—	1	36.00	—
69	—	—	—	—	—	—
70	—	—	—	—	—	—
71	—	—	—	1	32.00	—
72	—	—	—	—	—	—
73	—	—	—	1	31.00	—
74	—	—	—	1	32.00	—
75	—	—	—	1	33.00	—
76	—	—	—	—	—	—
77	—	—	—	—	—	—
78	—	—	—	—	—	—
79	—	—	—	—	—	—
80	—	—	—	1	35.00	—
81	—	—	—	—	—	—
82	—	—	—	—	—	—
83	—	—	—	—	—	—
84	—	—	—	1	30.00	—

Mortality

The results of this study demonstrate that total mortality (Z) is significantly less when section rather than surface ages are used for slow-growing, long-lived fishes such as *S. pinniger* and *S. diploproa* (Table 2). As evident in the larger reduction in Z for males versus females, the problem is more pronounced in males, possibly because their slower growth increases the difficulty of assigning accurate surface ages. This may explain why Z is higher in male *S. diploproa* than in females when surface ages are used and lower when section ages are used. The absence of older *S. pinniger* females also contributed to the smaller decrease in Z when section ages were used.

This study has documented important differences in estimates of growth and mortality which result solely from differences in otolith ageing methodology. It is hoped that subsequent research will incorporate these estimates into various stock assessment models to evaluate the effect that these different otolith ageing techniques have on models designed to evaluate yield and production characteristics of long-lived, slow-growing fish stocks.

ACKNOWLEDGMENTS

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LITERATURE CITED

Archibald, C. P., W. Shaw, and B. M. Leaman. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. 1048, 57 p.

Beamish, R. J. 1979a. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can., 36: 141–151.

Beamish, R. J. 1979b. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can., 36: 1395–1400.

Bennett, J. T., G. W. Boehlert, and K. K. Turekian. 1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from ^{210}Pb/^{226}Ra measurements in otoliths. Mar. Biol. (Berl.), 71: 209–215.

Boehlert, G. W. 1980. Size composition, age composition, and growth of canary rockfish, *Sebastes pinniger*, and splitnose rockfish, *S. diploproa*, from the 1977 rockfish survey. Mar. Fish. Rev., 42(3–4): 57–63.

Boehlert, G. W. 1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull., 83: 103–117.

Boehlert, G. W., and R. F. Kappenman. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser., 3: 1–10.

Boehlert, G. W., and M. M. Yoklavich. 1984. Variability in age estimates in *Sebastes* as a function of methodology, different readers, and different laboratories. Calif. Fish and Game, 70(4): 210–224.

Campana, S. E., K. C. T. Zwanenburg, and J. N. Smith. In press. ^{210}Pb/^{226}Ra determination of longevity in redfish. Can. J. Fish. Aquat. Sci.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 p.

Dark, T. A. 1975. Age and growth of Pacific hake, *Merluccius productus*. Fish. Bull., 73: 336–355.

Dark, T. A., M. E. Wilkins, and K. Edwards. 1983. Bottom trawl survey of canary rockfish (*Sebastes pinniger*), yellowtail rockfish (*S. flavidus*), bocaccio (*S. paucispinis*), and chilipepper (*S. goodei*) off Washington —California, 1980. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-48, 40 p.

Dixon, W. J. 1981. BMDP statistical software. Univ. Calif. Press, Berkeley, 726 p.

Gallucci, V. F., and T. J. Quinn II. 1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc., 108: 14–25.

Gulland, J. A. 1983. Fish stock assessment. A manual of basic methods. John Wiley and Sons, New York, 223 p.

Hirschhorn, G. 1974. The effect of different age ranges on estimated Bertalanffy growth parameters in three fishes and one mollusk of the northeastern Pacific Ocean. Pages 192–199 *In* T. B. Bagenal (ed.) The ageing of fish. Unwin Brothers, Surrey, Engl.

Knight, W. 1968. Asymptotic growth: An example of nonsense disguised as mathematics. J. Fish. Res. Board Can., 25: 1303–1307.

Leaman, B. M., and D. A. Nagtegaal. 1987. Age validation and revised natural mortality rate for yellow tail rockfish. Trans. Am. Fish. Soc., 116: 171–175.

Le Cren, E. D. 1974. The effects of errors in ageing in production studies. Pages 221–224 *In* T. B. Bagenal (ed.) The ageing in fish. Unwin Brothers, Surrey, Engl.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Regression, analysis of variance, and experimental designs. Richard D. Irwin, Inc., Homewood, Ill.

Nichy, F. 1977. Thin-sectioning fish ear bones. Fish age determination aids pollution control research. Sea Technol., Feb., p. 27.

Rao, C. R. 1973. Linear statistical inference and its implications. 2nd ed. John Wiley and Sons, New York, 625 p.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Shaw, W., and C. P. Archibald. 1981. Length and age data of rockfishes collected from B.C. coastal waters during 1977, 1978, and 1979. Can. Data Rep. Fish. Aquat. Sci. 289, 119 p.

Six, L. D. and H. F. Horton. 1977. Analysis of age determination methods for yellow tail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., 75: 405–414.

Vaughan, D. S., and P. Kanciruk. 1982. An empirical comparison of estimation procedures for the von Bertalanffy growth equation. J. Cons. Cons. Int. Explor. Mer, 40: 211–219.

Wilson, C. D. 1985. The effects of different otolith ageing techniques on estimates of growth and mortality for two species of rockfishes, *Sebastes pinniger* and *Sebastes diploproa*. M.S. Thesis, Oregon State Univ., Corvallis, 107 p.

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Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis

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ABSTRACT: Daily increments in otoliths were used to estimate growth rates and hatch dates of young walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska, USA. Growth rate increased through the first 70 d after hatching and was described by a nonlinear, Laird-Gompertz model. There were no interannual differences in growth rates of young larvae from the limited size range collected in 1983 and 1985 to 1987. Growth rates of older larvae and pelagic juveniles increased from southwest to northeast along the Alaskan Peninsula. Hatch dates were calculated from age of fish at time of collection; spawning dates were estimated after accounting for temperature-dependent egg stage duration. From 1983 to 1987, spawning and hatch dates seem to have shifted to later in the season. This can indicate an overall change in time of spawning or increased removal, through mortality and dispersal, of eggs and larvae spawned early in the season. Hatch dates were earlier in the southwest near Unimak Island and later in the season to the northeast around Kodiak Island. Mortality was estimated from the difference in abundance of each daily cohort between the May and June-July surveys in 1987 and was age dependent. Mean daily instantaneous mortality rate was 0.11 for young larvae and decreased to 0.02 for older larvae and pelagic juveniles. From these rates, it is estimated that about 97 % of the larvae will die or be removed from the Shelikof Strait area within 35 d of hatching.

INTRODUCTION

Survival and recruitment of young fishes depends on the combined action of biological and physical factors such as starvation, predation, larval transport, temperature, and turbulence. Larval size and growth are particularly important to the recruitment process because size is linked with resistance to starvation and predation (Miller et al. 1988), while small changes in growth rate and larval stage duration can cause significant interannual fluctuations in recruitment (Houde 1987).

Daily increments of otoliths provide a powerful tool to study growth and survival of larval and juvenile fishes. Increment counts have been used to estimate age of larval fish from the field (see review by Campana & Neilson 1985); the resultant growth rates have been examined in terms of environmental (Methot & Kramer 1979), geographical (Nishimura & Yamada 1988), and interannual (Nyman & Conover 1988, Warlen 1988) variability. Distributions of hatch dates, estimated from ages of larvae at the time of collection, can define periods of successful spawning relative to environmental conditions (Methot 1983, Checkley et al. 1988, Nyman & Conover 1988). Successful spawning sites can be identified using rates and direction of ocean currents in conjunction with hatch dates. Survival of larval fish has been estimated from differences in hatch-date frequency distributions (Methot 1983, Essig & Cole 1986, Rice et al. 1987).

In terms of biomass, walleye pollock *Theragra chalcogramma* has been the world's largest single-species commercial fishery since 1973 [Food and Agriculture Organization (FAO) 1974], with 1.6 million metric tons (t) harvested in 1986 in Alaskan waters (FAO 1988). Ichthyoplankton surveys conducted in the Shelikof Strait and surrounding areas of the western Gulf of Alaska since 1972 (Dunn & Rugen 1989) have provided information on the early life history of walleye pollock (Kendall et al. 1987, Kim 1987). Most spawning is

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expected to occur during a 2 wk period from late March to early April in the deep water of Shelikof Strait. Eggs remain deep in the water column and hatch in approximately 2 wk at a depth of about 150 m. Larvae begin to feed 5 to 6 d after hatching and then are found primarily in the upper 50 m of the water column where they are subject to transport by currents flowing toward the southwest at speeds from 5 to 30 cm s^{-1}. Cohorts of eggs and larvae form large aggregations that can be followed both spatially and temporally for several weeks. Young-of-the-year juveniles inhabit areas downstream, along the continental shelf of the Alaskan Peninsula (Hinckley et al. 1989). These circumstances provide a unique opportunity to assess rates of growth and mortality during the early life of this species.

Using age and hatch-date distributions derived from otoliths of young walleye pollock collected in the Shelikof Strait and surrounding areas, our objectives were (1) to describe the growth rate throughout early life, (2) to assess interannual and geographical differences in growth rates and in successful spawning dates, and (3) to estimate mortality.

METHODS

Larval and juvenile collections. Young walleye pollock larvae (< 46 d old) were collected during ichthyoplankton surveys in the Shelikof Strait region of the western Gulf of Alaska in May of 1983 and 1985 to 1987. Collection techniques followed Kendall et al. (1987); briefly, samples were taken with a double-oblique tow using a 60 cm bongo net (333 or 505 µm mesh). In 1987, older larval and pelagic juvenile walleye pollock (from 36 to 85 d old) were collected at 148 stations throughout the western Gulf of Alaska, beginning near Unimak Island on 18 June and terminating northeast of Kodiak Island on 16 July. Fish were sampled using a 5 m^2 Methot frame trawl (Methot 1986) equipped with oval mesh (2×3 mm). The net was deployed from the NOAA ship 'Miller Freeman' and retrieved obliquely from a maximum depth of 300 m (Hinckley et al. 1989). Subsamples of fish were preserved in 95 % buffered ethanol for otolith examination.

For each survey, the number of fish per tow was standardized to number under 10 m^2 of sea surface. Standard length (SL, to the nearest 0.1 mm) was measured from random subsamples of formalin-preserved fish taken at each station. Length distributions were expanded to the total catch at each station. Size was not corrected for possible shrinkage due to collection or fixation techniques.

Age and growth determination. In May 1983, larvae were collected for age and growth determination from 5 locations, including the area of highest larval abundance (Fig. 1A). Limited numbers of larvae were collected for ageing studies in May 1985 and 1986 (Fig. 1B, C). Larvae were obtained for age analysis from 13 stations throughout the survey area in May 1987 (Fig. 1D). Otoliths were removed and SL (to the nearest 0.1 mm) was measured from fish of the entire range of sizes within each sample.

Otolith increment deposition is daily for larval and juvenile walleye pollock to at least 100 d, with a well-defined increment formed at hatching (Nishimura & Yamada 1984, Bailey & Stehr 1988). Age was determined using techniques reported in Kendall et al. (1987). The ages of larvae from the 1983 samples have been previously reported in Kendall et al. (1987).

Age and growth were determined for older larvae and pelagic juveniles from Unimak Island to Kodiak Island, including fish from the area of highest density, between the Semidi and Shumigin Islands (Fig. 2). Both sagittae were removed, and thin sections in the sagittal plane were prepared for age determination, using techniques described by Boehlert & Yoklavich (1985). Otolith sections were covered with immersion oil, and growth increments were counted at 1000 × magnification using a compound microscope and transmitted light. In most cases, both otoliths from each fish were examined and the higher number of increments was used to estimate age. Most increment widths were greater than 1 µm, and groups of narrowly spaced increments having widths below the theoretical limits of resolution by light microscopy [calculated by Campana et al. (1987) to be 0.2 µm] were not evident. Increment counts from otoliths from a broad size range of larvae were confirmed by a second reader.

Age and length data from young larvae were plotted over all stations within each survey to determine growth rates and hatch dates. Preliminary examination of the otoliths of the older larvae and pelagic juveniles collected in June and July 1987 indicated that increment widths were narrower in otoliths from the southwest near Unimak Island and wider in otoliths from the northeast around Kodiak Island, suggesting possible differences in larval growth between locations. We therefore separated the data into 3 areas: (1) stations located off Unimak Island at the most southwest point of the survey; (2) stations between the Semidi and Shumigin Islands, representing the area of highest fish abundance; and (3) stations around Kodiak Island (Fig. 2).

Hatch-date distributions. Hatch dates were estimated from age and date of capture. Length-frequency distributions, representing total, standardized abundances of fish at each station, were converted to age using separate age-length keys (Kimura 1977) developed from subsamples of fish at selected stations

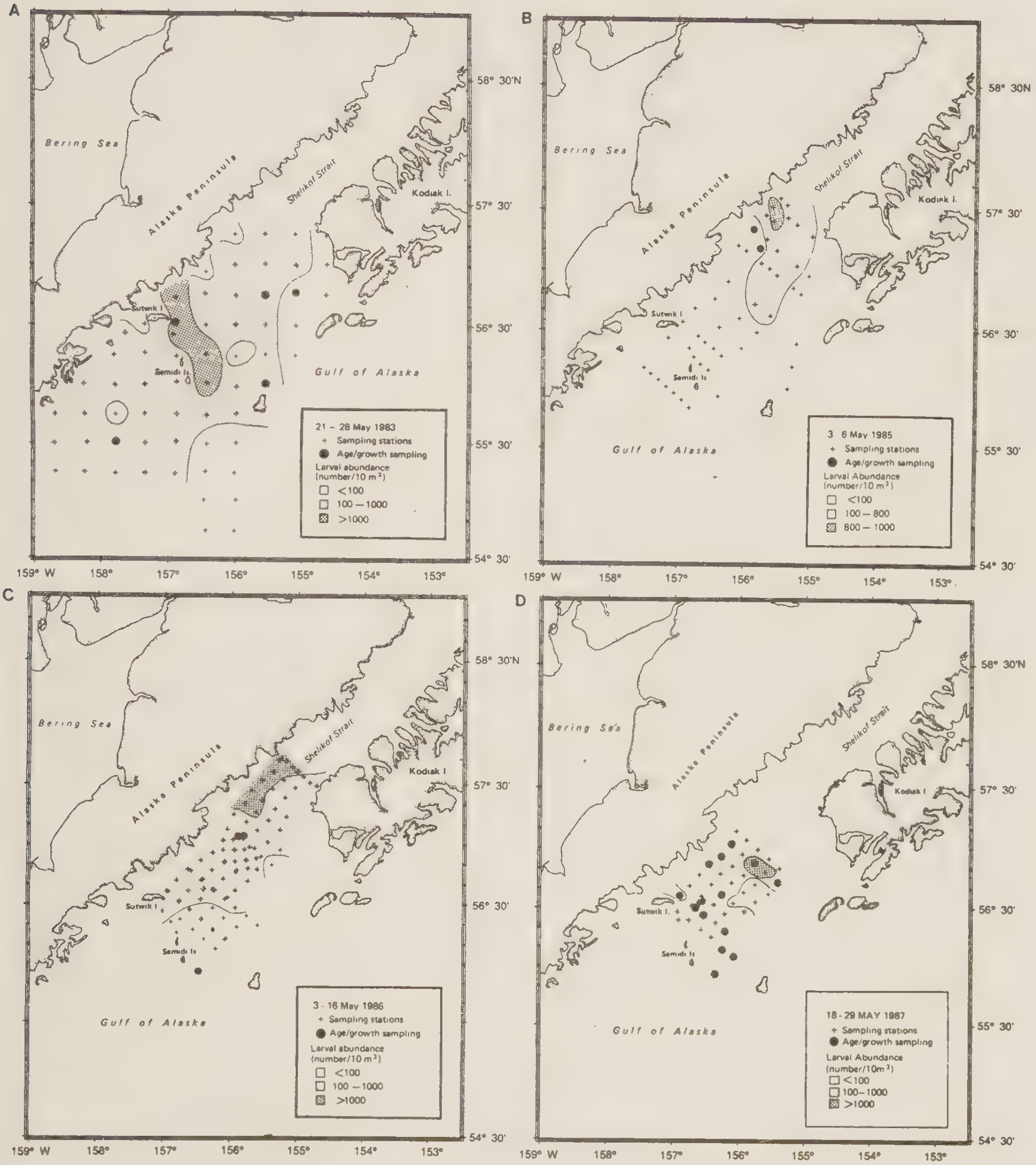
A
Bering Sea
Alaska Peninsula
Shelikof Strait
Kodiak I.
Sutwik I.
Semidi Is.
Gulf of Alaska
21 - 28 May 1983
+ Sampling stations
● Age/growth sampling
Larval abundance (number/10 m²)
☐ <100
☐ 100—1000
▨ >1000
B
Bering Sea
Alaska Peninsula
Shelikof Strait
Kodiak I.
Sutwik I.
Semidi Is
Gulf of Alaska
3 6 May 1985
+ Sampling stations
● Age/growth sampling
Larval Abundance (number/10 m²)
☐ <100
☐ 100—800
▨ 800—1000
C
Bering Sea
Alaska Peninsula
Shelikof Strait
Kodiak I
Sutwik I
Semidi Is
Gulf of Alaska
3 - 16 May 1986
+ Sampling stations
● Age/growth sampling
Larval abundance (number/10 m²)
☐ <100
☐ 100 —1000
▨ >1000
D
Bering Sea
Alaska Peninsula
Shelikof Strait
Kodiak I
Sutwik I.
Semidi Is
Gulf of Alaska
18 - 29 MAY 1987
+ Sampling stations
● Age/growth sampling
Larval Abundance (number/10m²)
☐ <100
☐ 100—1000
▨ >1000
58° 30'N
57° 30'
56° 30'
55° 30'
54° 30'
159° W
158°
157°
156°
155°
154°
153°

Fig. 1. Locations of larval walleye pollock collections in the western Gulf of Alaska during May of (A) 1983, (B) 1985, (C) 1986, and (D) 1987

within each survey and for each of the 3 areas within the June-July 1987 survey. Hatch-date distributions were generated from these computed age distributions.

For seasonal and interannual comparisons, hatch-date distributions were corrected for mortality because fish that hatched closer to the time of collection experienced less mortality than older fish in the samples. Size-specific mortality rates of larval and juvenile walleye pollock were unknown a priori. We therefore combined field mortality rates for small walleye pollock

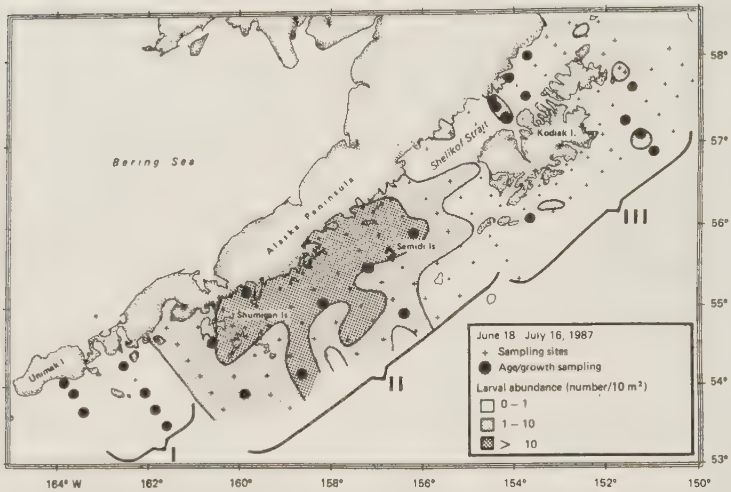

Fig. 2. Locations of sampling sites of older walleye pollock larvae and pelagic juveniles in the western Gulf of Alaska during June and July 1987. Areas used in geographic comparisons of growth rates and hatch dates are designated I, II, and III

larvae, ranging from 0.096 d^{-1} for larvae 4 to 5 mm SL and 0.082 d^{-1} for larvae 8 to 9 mm SL (Kim 1987) to 0.062 d^{-1} for larvae less than 15 mm SL (Reed et al. 1989), with those for larger marine fish larvae calcuIN RUHEated from a general equation of mortality on weight reported by McGurk (1986), and a length-weight relationship for larval walleye pollock (Bailey & Stehr 1986). A stepped size-specific mortality function was created, with rates of: 0.10, 0.08, 0.06, 0.03, 0.01 d^{-1} for fish 4–7, 7.1–10, 10.1–15, 15.1–20 and 20.1–30 mm SL, respectively. The range of ages corresponding to each mortality rate was calculated from our 1987 growth equation. This age-specific mortality correction generally resulted in a redistribution of hatch date frequencies, especially in those collections with the widest ranges of ages (i.e. from 1983 and 1987).

Mortality estimates. Daily instantaneous mortality rates were calculated from the difference in the abundance of each daily cohort between the May and June 1987 surveys. Note that these estimates were not corrected with the size-selective mortality function mentioned in the previous section. Abundance was adjusted beforehand using the Sette-Ahlstrom census method (Richardson 1981) in which the number of fish under 10 m^2 of sea surface was weighted by the area represented by each station. Mortality rates (Z_i) were calculated as:

$$Z_i = -[\log_e(N_{J_i}/N_{M_i})]t^{-1}$$

where N_{J_i} is the number of fish collected in June that hatched on Day i; N_{M_i} is the number of fish collected in May that hatched on Day i; and t = 38 d (the time interval between median dates of each survey).

RESULTS

Age and growth

Ages of 638 larval and pelagic juvenile walleye pollock from the western Gulf of Alaska ranged from 3 to 85 d (Table 1). From the 1987 collections, 357 young walleye pollock were considered for intra-annual assessment of age and growth throughout early development. These included 204 larvae (3.9 to 11.2 mm SL) from the May collections and 153 older larvae and pelagic juveniles (12.8 to 30.0 mm SL) from the June and July collections in Area II. Otolith increment counts (days since hatching) ranged from 3 to 34 for the larvae collected in May, and from 36 to 66 for the older fish.

Estimated age and length data from the May and June-July 1987 (Area II only) collections were combined and growth was described with a nonlinear Laird-Gompertz function, using Marquardt's algorithm as implemented in SYSTAT (Wilkinson 1987):

$$L_t = 4.505\ [e^{7.854(1-e^{-0.004t})}]$$

where L_t = standard length (mm) at age t (days from hatch; Fig. 3). An approximate coefficient of determination (r^2) is 0.95. The model suggests that growth rate of young walleye pollock is relatively slow to an age of about 20 d, with a mean absolute growth rate of about 0.16 mm d^{-1} during the first 10 d post-hatching; growth rate accelerates with age to about 0.66 mm d^{-1} for 60- to 70-d-old fish. Larval length at time of hatching was estimated by the model to be 4.5 mm, which approximates the mean length of live walleye pollock hatched

Table 1. *Theragra chalcogramma.* Information on larval and juvenile collections in the western Gulf of Alaska. Values in parentheses are percentages; age and length ranges given

Collection date	No. caught	No. measured	No. aged	Aged specimens Age (d)	Aged specimens Length (mm)
21–28 May 1983	4136	1919 (47)	109 (3)	7–46	6.0–14.7
1–12 May 1985	321	258 (80)	25 (8)	6–23	5.8– 9.0
3–16 May 1986	12803	4239 (33)	76 (0.6)	3–14	5.2– 8.7
18–29 May 1987	2571	1740 (68)	204 (8)	3–34	3.9–11.2
18–19 Jun 1987 (Area I)	37	34 (92)	36 (97)	39–75	12.9–25.7
19 Jun–10 Jul 1987 (Area II)	4699	1729 (37)	153 (3)	36–66	12.8–30.0
10–15 Jul 1987 (Area III)	95	86 (91)	35 (37)	42–85	16.8–40.8

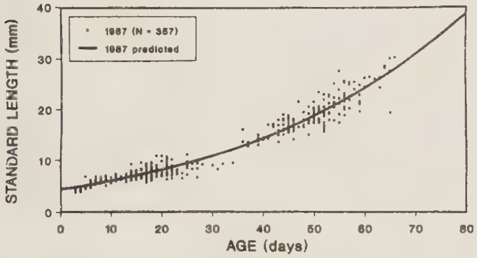

Fig. 3. *Theragra chalcogramma.* Estimated age versus length for larval and juvenile walleye pollock collected in May and June-July 1987 (only Area II). The line represents a least-squares fit of the Laird-Gompertz growth model: $L_t = 4.505e^{7.854(1-e^{-0.004t})}$

in the laboratory from eggs collected in the study area (4.3 mm SL; M. Yoklavich unpubl.).

A least-squares linear model, length = *a* + *b*(age), was fitted to each of the 4 sets of age-length data from the years 1983 and 1985 to 1987, over the limited range of ages common to all sets. A linear model was used to facilitate interannual growth rate comparisons and adequately fit the data because of the narrow age ranges. No differences in growth rates were found (analysis of covariance i.e. ANCOVA, $p > 0.078$). Sample sizes were small because of narrow ranges in age of the 1985 and 1986 fish (Table 1). A comparison of the data sets with the broadest ranges of ages, those collected in 1983 [a year of relatively high walleye pollock spawning biomass (Megrey 1989)] and those from 1987 (a year of low spawning biomass), also indicated no difference in growth rate over common ages (7 to 25 d; ANCOVA, $p > 0.703$). In all possible pairwise comparisons among the 4 years of data, using those ages common to each comparison, there were no differences in growth rates.

Growth rates were assessed for older larvae and pelagic juveniles collected in June and July 1987 from the 3 areas described earlier (Fig. 4). A least-squares linear model was used to describe growth from the 3 sets of age and length data, over those ages (42 to 66 d old) common to all areas. Although Areas I and III represent fewer fish, significant (ANCOVA, $p < 0.001$) differences were found among areas; mean absolute growth rate was slowest (0.30 mm d^{-1}) in the southwest and increased to the north with mean rates of 0.48 mm d^{-1} in the main aggregation and 0.82 mm d^{-1} from fish collected near Kodiak Island.

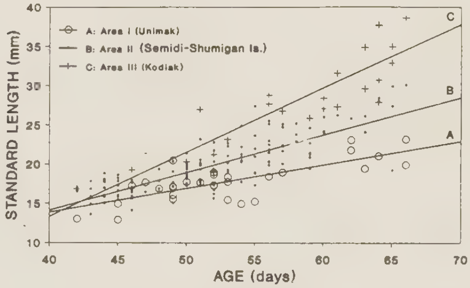

Fig. 4. *Theragra chalcogramma.* Growth of walleye pollock collected in June and July 1987. Regression models relating length (L) and age (a) are (A) $L = 1.81 + 0.30a$, $r^2 = 0.59$, $N = 31$; (B) $L = 0.48a - 4.92$, $r^2 = 0.66$, $N = 139$; and (C) $L = 0.82a - 19.24$, $r^2 = 0.78$, $N = 24$

Hatch-date distributions

Hatch-date distributions were compared between early larvae collected in May 1987 and the older fish collected from Area II in June and July 1987 (Fig. 5). Both distributions have similar ranges of hatch dates (16 April to 24 May and 7 April to 26 May, respectively) and comparable median hatch dates (i.e. 2 May and

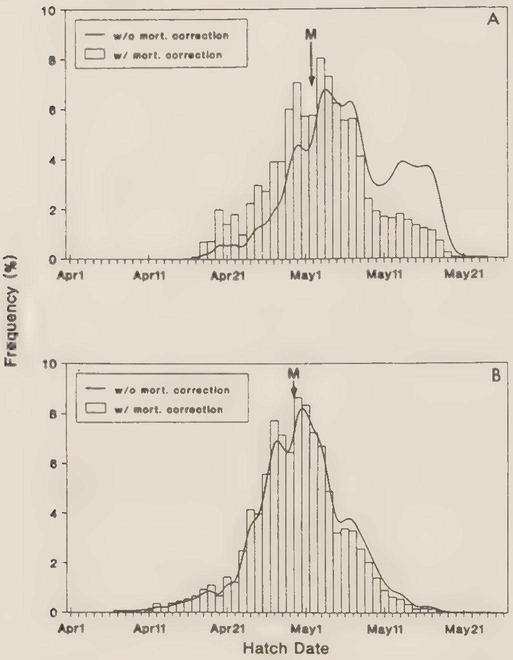

Fig. 5. *Theragra chalcogramma*. Hatch date distributions estimated from age of walleye pollock collected in (A) May 1987 and (B) June-July 1987. Bars represent frequencies corrected for differential mortality (i.e. w/mort. correction; see text); continuous lines are the frequency distributions without mortality corrections (i.e. w/o mort. correction). Median dates (M) are also indicated

29–30 April, respectively, from distributions with mortality corrections), supporting the contention that they represent the same cohort of spawned eggs. There is a noticeable decrease, however, in the relative number of fish hatched late in the season, with 58 % of the fish collected in May hatching after 1 May, and only 37.5 % of the older larvae collected in June and July having hatch dates after this date (77 and 42 %, respectively, from distributions without mortality corrections).

A distinct shift toward later hatch dates for walleye pollock collected in May is evident over the 4 years considered (Fig. 6). This trend is demonstrated in the delayed median hatch dates and increased percentage of larvae in the 1986 and 1987 collections that hatched after 1 May (Table 2).

Median spawning dates were estimated from the hatch dates and egg incubation period (Table 2). Duration of the egg stage depends upon bottom water temperature in Shelikof Strait in March and April and was calculated from the relation between temperature and hatching-time reported by Haynes & Ignell (1983).

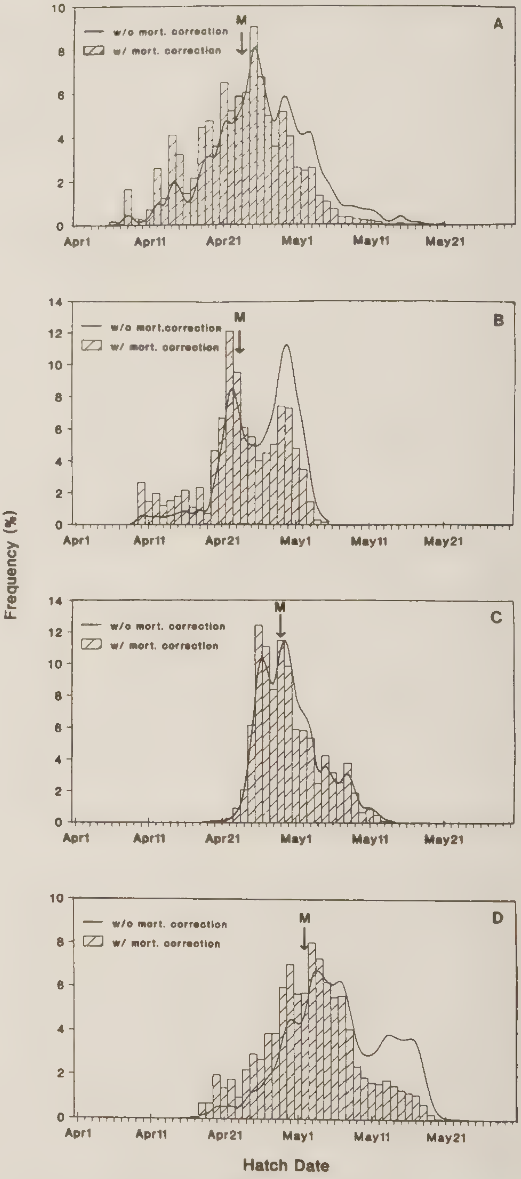

Fig. 6. *Theragra chalcogramma*. Hatch date distributions, based upon age, of young walleye pollock collected in May (A) 1983, (B) 1985, (C) 1986, and (D) 1987. See Fig. 5 for further details

Egg surveys conducted in Shelikof Strait describe peak spawning time as the first week in April, with continued spawning of less intensity through May (Kim 1987). Peak spawning in 1983 and 1985, predicted from

Table 2. *Theragra chalcogramma.* Median spawning (M_S) and hatch (M_H) dates for larvae collected during May in the western Gulf of Alaska

Year	M_S	M_H	% hatch after May 1	Days to hatch	Bottom temp. (°C)[a]
1983	10 Apr	23 Apr	10	13	5.5
1985	9 Apr	23 Apr	5	14	5.3
1986	15 Apr	29 Apr	32	14	5.0
1987	20 Apr	2 May	58	13	5.6

[a] J. Schumacher unpubl.

age of larvae, was comparable to that expected from egg surveys. The median spawning date predicted for 1986 was nearly a week later. In 1987, the median spawning date, predicted from the ages of surviving larvae, was 20 April.

Hatch-date distributions estimated from ages of the larvae collected in June and July 1987 indicated earlier hatching in the southwest near Unimak Island (median date of 25 April) and later hatching to northeast around Kodiak Island (median date of 8 May; Fig. 7). Distributions from these 2 areas appeared multi-modal. Eight percent of the larvae collected in Area I had hatch dates in late March, 37 % represented hatching in early April, and 55 % hatched in late April or early May (Fig. 7C). Sixty-eight percent of the larvae found in Area III hatched from 24 April to 14 May; smaller amounts of hatching occurred in mid-April (8 %) and late May (24 %; Fig. 7A).

Mortality

Daily instantaneous mortality rates, calculated from the difference in area-adjusted hatch date distributions between the May and June-July surveys in 1987, increased throughout the hatching period (Fig. 8). Mortality rate appears to be a function of age and size of the fish at capture. For example, the highest mortality rates, averaging 10 to 11 % d^{-1}, were experienced by the youngest larvae whose hatch dates were nearest to the date of collection (Table 3). Mortality rate decreased steadily with increased length and age of larvae. Cumulative larval mortality during the first 35 d was estimated at about 93 %.

DISCUSSION

Our otolith data, combined with the opportunity to track aggregations of walleye pollock larvae through time in the Alaska Coastal Current, allow us to make realistic estimates of growth and mortality during the early life of this species. These estimates will make possible the assessment of interannual variability in early survival and its role in recruitment of walleye pollock stocks. In the broader context of marine ecology, the ability to make precise estimates of growth and mortality by ageing larval fish from otoliths is unparalleled in other planktonic organisms, and can be useful in the analysis of size-scaled processes of marine organisms (Peterson & Wroblewski 1984).

Growth rates of larval walleye pollock based on otolith analysis increase throughout the first 70 d post-hatching. Most larval walleye pollock are concentrated between 15 and 50 m in Shelikof Strait (Kendall et al. 1987). Because water temperature in the upper 50 m of our survey area increased from around 5 °C during the larval stage to over 8 °C during the early juvenile period (J. Schumacher unpubl.), it is difficult to discriminate between the effects of temperature and developmental stage on growth rate. With appropriate temperature records collected during early larval development each year, an age- and temperature-based growth model similar to that recently developed for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine (Campana & Hurley 1989) could be applied to future growth studies of walleye pollock larvae in the Gulf of Alaska. In general, mean water temperature at 50 m depth in Shelikof Strait was similar in May of 1983, 1985, and 1987 (5 to 6 °C). Although mean water temperature at 50 m in May of 1986 was relatively cold (3.3 °C; J. Schumacher unpubl.), the growth rate of young larvae collected downstream from Shelikof Strait did not differ significantly from rates in the other years.

Our growth rates are comparable to those estimated for walleye pollock larvae of the same age held in the laboratory at 9 to 11 °C with abundant food (Bailey & Stehr 1986). This suggests that surviving larvae obtain enough food in the field for adequate growth. Yamashita & Bailey (1989) reported high mortality rates for young larvae held in low prey densities during the first-feeding transition, indicating that larvae exposed to episodic food limitations may not survive to be sampled in the field. Growth rates similar to ours also were

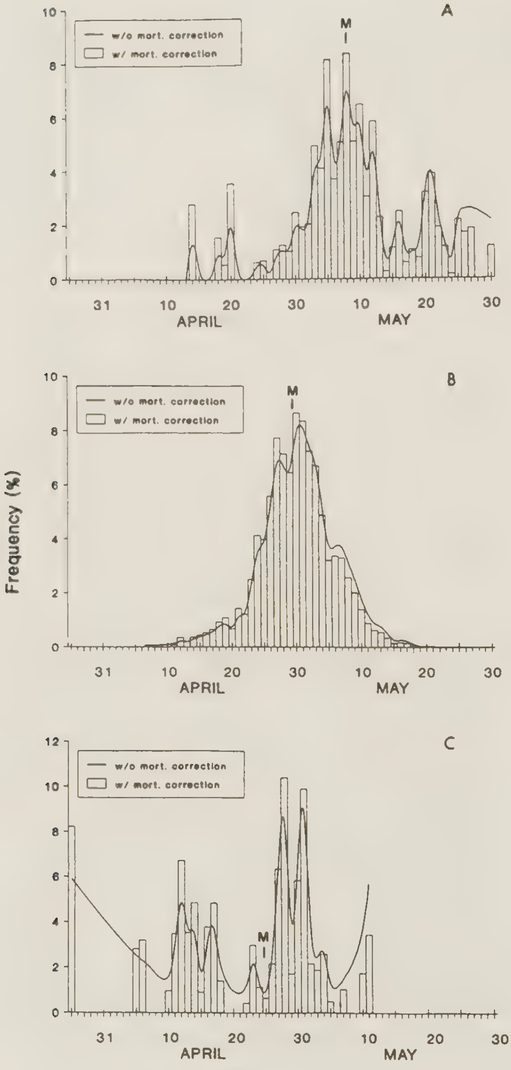

Fig. 7. *Theragra chalcogramma*. Hatch date distributions, based upon age of older larvae and juveniles of walleye pollock collected in June-July 1987 (A) near Kodiak Island, (B) between the Semidi and Shumigin Islands, and (C) near Unimak Island. See Fig. 5 for further details

reported for larval and juvenile walleye pollock collected from the waters around Hokkaido, Japan (Nishimura & Yamada 1984, 1988).

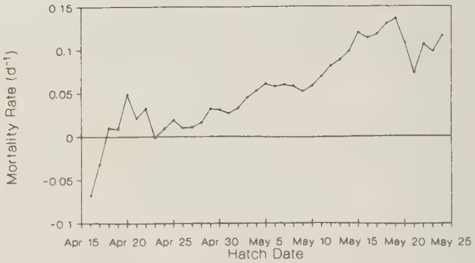

Fig. 8. *Theragra chalcogramma*. Instantaneous daily mortality rates by hatch date for larval walleye pollock in the western Gulf of Alaska

Density-dependent larval growth is considered one of the likely causes of the asymptotic relationship between recruitment and the parent stock (Shepherd & Cushing 1980). Although an asymptotic or dome-shaped stock-recruitment relationship has been observed for walleye pollock in the western Gulf of Alaska (Megrey 1989), we found no evidence of density-dependent growth of young larvae. Adult biomass of walleye pollock in the Shelikof Strait region, estimated from hydroacoustic and bottom trawl surveys, has declined continually from a peak of 3.4×10^6 t in 1981 to 2.2×10^6 t in 1983 and about 0.3×10^6 t in 1988 (Megrey 1989). A general decline in larval abundance also is apparent from 1981 to 1987 (from about 10×10^{11} to 3.8×10^{11} larvae; S. Picquelle pers. comm., K. Bailey unpubl.), although comparisons are difficult considering potential differences in larval age and survey dates. The lack of interannual differences among growth rates for 1983 and 1985 to 1987 does not support the density-dependent growth hypothesis for walleye pollock larvae.

Although interannual differences in growth were not discerned for young larvae, the potential for spatial and temporal variation in growth was demonstrated for older larvae and pelagic juveniles. Growth rates increased significantly from southwest to northeast along the Alaska Peninsula. Collections were initiated in June in the southwest and terminated in mid-July in the northeast; water temperature in the upper 50 m increased from about 5 °C in mid-June to over 8 °C in early July (J. Schumacher unpubl.). Nishimura & Yamada (1988) reported a marked increase in growth for young walleye pollock hatched later in the season in the Okhotsk Sea and suggested that rapid growth may correspond to increasing water temperature during larval development.

Changes in time of spawning can contribute to variations in year-class abundance by influencing the spatial and temporal coincidence of larvae, prey availability, predator abundance, and favorable environmental conditions, such as temperature and upwelling (Cushing 1975, Parrish et al. 1981). Median spawning and hatch dates of surviving walleye pollock larvae differ

Table 3. *Theragra chalcogramma*. Mean daily instantaneous mortality coefficients (Z) estimated from hatch date distributions of larval walleye pollock from the May and June 1987 surveys. Mean (and range) in length and age of larvae of time of capture are reported by hatch date

Hatch date	May		June		Z	Percent mortality (d^{-1})
	Size (mm)	Age (d)	Size (mm)	Age (d)		
16–19 Apr	10 (8–13)	33 (31–39)	26 (19–39)	65 (63–80)	–0.02	−2.1
20–27 Apr	9 (7–13)	28 (23–27)	23 (17–36)	60 (53–77)	0.02	1.8
28 Apr–6 May	8 (6–11)	19 (14–28)	21 (15–34)	53 (44–74)	0.04	3.9
7–10 May	7 (6–10)	14 (10–20)	19 (14–30)	45 (40–65)	0.06	5.5
11–15 May	6 (5–10)	8 (5–16)	17 (13–27)	42 (36–61)	0.09	8.7
16–22 May	5 (4–7)	4 (3–11)	16 (12–25)	40 (33–56)	0.11	10.6
23–24 May	4 (4–5)	4 (3–4)	16 (15–19)	48 (45–49)	0.11	10.2

interannually by about 2 wk, and in recent years have progressively shifted to later in the season. Although larvae were sampled earlier in the season in 1985 and 1986 (Table 1), and from more limited areas of their distribution (Fig. 1), the hatch-date distributions from these years are consistent with the trend established from age data in 1983 and 1987 (years of comparable sampling dates and areal representation).

The mortality corrections that we implemented in the hatch date analysis are approximations based on available data. These corrections realistically could be underestimated by as much as a factor of 2 (errors associated with measurements of mortality are discussed later). A simple simulation with double mortality corrections for all age groups in both 1987 surveys (i.e. May and June-July) resulted in median hatch dates similar to the original corrected distributions. However, this simulation did redistribute the hatch dates from the May survey, thereby reducing the number of larvae hatched late in the season and producing a distribution closer to that of the June-July survey. This indicates that our mortality correction factors likely were conservative, especially for the young age groups.

Hatch-date distributions were used to examine transport and mortality of larvae. Current speeds in the Shelikof Strait region typically vary from 5 to 30 cm s^{-1} during the months when walleye pollock eggs and larvae are present; the more vigorous southwestward flow occurs in the Alaska Coastal Current, while weak and sometimes reversed flow is found along the Alaska Peninsula (Incze et al. 1989). The marked down-current progression of earlier larval hatch distributions from the June-July 1987 survey (Fig. 7) is indicative of significant southwestward advection of eggs and younger larvae spawned in the Shelikof Strait. Earliest hatch dates were observed for larvae collected near Unimak Island, an area farthest from the proposed spawning site near Cape Kekurnoi. The fast-growing larvae collected around Kodiak Island were most recently spawned (82 % after 15 April).

The similarity in hatch distributions of larvae collected from the main aggregations in May 1987 and June-July 1987 (Fig. 5) indicates that the 2 surveys sampled the same larval cohort. Furthermore, the median age of larvae from the May collection is 16 d; median age of older larvae collected in June and July is 54 d. The difference in median age of the 2 groups of larvae is 38 d and equal to the interval of time between median sampling dates of the 2 surveys. The centers of abundance for these 2 collections are about 200 km apart, suggesting a larval transport rate of about 5 km d^{-1}. This is considered to be a moderate current speed in this area of the Gulf at this time of year (Incze et al. 1989), and demonstrates the likelihood that the aggregation of larvae collected early in the season northeast of the Semidi Islands is the same cohort of older larvae found along the Alaskan Peninsula in June and July. The movement of satellite-tracked drifters, drogued at 40 m and released in the main spawning area in April 1987, also supports the assumption that the May and June-July aggregations represent the same cohort (Hinckley et al. 1989).

Assumptions in our assessment of mortality are that diffusion of larvae is not influencing the estimate of total abundance, and that coverage of the area of each daily cohort's distribution is complete in both surveys. Although eddy diffusivity can be important in this area, it is probably compensated to varying degrees by horizontal convergence (Reed et al. 1989). Furthermore, sampling a much broader area during the June-July survey should account for surviving larvae from the May survey, thereby reducing possible effects of advective or diffusive losses from the sampling boundary. The downstream increase in larval age and the observance that fish at the most southwest area of the June-July survey hatched earlier than those in the May survey further indicates that the larvae surveyed in May were encompassed by the later survey.

The absence of a clear gradient of larval concentrations outside the area of highest abundance during the early survey (Fig. 1D) suggests incomplete sampling, most likely of the older larvae that have drifted from the center of spawning activity. Underestimating the number of older larvae during the May survey leads to negative mortality rates for larvae (8 to 13 mm) with the earliest hatch dates (Fig. 8, Table 3). Along with possible dispersal of the oldest larvae from the May survey, avoidance of the bongo nets by the largest larvae sampled during May could also contribute to the negative mortality rates for the oldest fish. However, comparisons of length frequencies of larval walleye pollock between day and night and between 1 m Tucker trawl and 60 cm bongo samples did not indicate size-selective avoidance (Kendall et al. 1987). The variable mortality rates among the smallest larvae hatched after 20 May (Fig. 8) indicate under-representation of this group in the May survey, possibly due to extrusion of some yolk-sac larvae from the 505 µm mesh bongo nets. Our future analyses of data from 1988 and 1989 ichthyoplankton surveys will yield more precise estimates of larval mortality and the combined effects of advection, eddy diffusivity, and horizontal convergence. Our values of average daily mortality occurring in the interim between the 2 surveys are comparable to those estimated for aggregated sizes of young larval walleye pollock collected in Shelikof Strait (Kim 1987, Reed et al. 1989), as well as for other gadid species of the same early life stages (Gamble & Houde 1984, Houde 1987). Although our estimates of mortality were relatively high during the earliest larval stages, they were much lower than those predicted by McGurk's (1986) general equation based on larval dry weight [e.g. from 1.31 d^{-1} for larvae at 36.1 µg (about 4 mm SL) to 0.18 d^{-1} for larvae at 380 µg (8 mm SL)]. Our rates were somewhat higher than those predicted by Peterson & Wroblewski's (1984) model of mortality rates for marine organisms.

Relatively small changes in growth and mortality rates could cause significant changes in recruitment, as suggested for Atlantic cod (*Gadus morhua*; Houde 1987). The low growth rates, which imply long stage duration, and relatively high mortality rates during the early ontogeny of walleye pollock indicate that fluctuations in recruitment may be controlled during the early larval stage.

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LITERATURE CITED

Bailey, K. M., Stehr, C. L. (1986). Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. exp. mar. Biol. Ecol. 99: 233–246

Bailey, K. M., Stehr, C. L. (1988). The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). J. exp. mar. Biol. Ecol. 122: 147–161

Boehlert, G. W., Yoklavich, M. M. (1985). Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. Fish. Bull. U.S. 83: 475–481

Campana, S. E., Gagne, J. A., Munro, J. (1987). Otolith microstructure of larval herring (*Clupea harengus*): image or reality. Can. J. Fish Aquat. Sci. 44: 1922–1929

Campana, S. E., Hurley, P. C. .F (1989). An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish Aquat. Sci. 46: 603–613

Campana, S. E., Neilson, J. D. (1985). Microstructure of fish otoliths. Can. J. Fish Aquat. Sci. 42: 1014–1032

Checkley, D. M., Jr, Raman, S., Maillet, G. L., Mason, K. M. (1988). Winter storm effects on the spawning and larval drift of a pelagic fish. Nature, Lond. 335: 346–348

Cushing, D. H. (1975). Marine ecology and fisheries. Cambridge University Press, Cambridge

Dunn, J. R., Rugen, W. C. (1989). A catalog of Northwest and Alaska Fisheries Center ichthyoplankton cruises 1965–1988. NWAF C Processed Rep. 89-04. Alaska Fish. Sci. Cent., Seattle

Essig, R. J., Cole, C. F. (1986). Methods of estimating larval fish mortality from daily increments in otoliths. Trans. Am. Fish. Soc. 115: 34–40

Food and Agriculture Organization (1974). Catches and landings, 1973. Yearbook of Fishery Statistics 36, FAO, Rome

Food and Agriculture Organization. (1988). Catches and landings, 1986. Yearbook of Fishery Statistics 62, FAO, Rome

Gamble, J. C., Houde, E. D. (1984). Growth, mortality and feeding of cod (*Gadus morhua* L.) larvae in enclosed water columns and in laboratory tanks. In: Dahl, E., Danielssen, D. S., Moksness, E., Solemdal, P. (eds.). The propagation of cod *Gadus morhua* L. Institute of Marine Research, Flodevigen Biological Station, Flodevigen Rapportserie 1, Arendal, Norway, p. 123–143

Haynes, E. G., Ignell, S. E. (1983). Effect of temperature on rate of embryonic development of walleye pollock, *Theragra chalcogramma*. Fish. Bull. U.S. 81: 890–894

Hinckley, S., Bailey, K., Schumacher, J., Picquelle, S., Stabeno, P. (1989). Preliminary results of a survey for late-stage larval walleye pollock and observations of larval drift in the western Gulf of Alaska, 1987. In: Proceedings of the international symposium on the biology and management of walleye pollock. Univ. of Alaska Sea Grant Rep. Ak-SG-89-01, Fairbanks, p. 297–306

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29

Incze, L. S., Kendall, A. W., Jr, Schumacher, J. D., Reed, R. K. (1989). Interactions of a mesoscale patch of larval fish (*Theragra chalcogramma*) with the Alaska Coastal Current. Contin. Shelf Res. 9: 269–284

Kendall, A. W., Jr, Clarke, M. E., Yoklavich, M. M., Boehlert, G. W. (1987). Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. U.S. 85: 499–521

Kim, S. (1987). Spawning behavior and early life history of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska, in relation to oceanographic factors. Ph. D. dissertation, Univ. Washington, Seattle

Kimura, D. K. (1977). Statistical assessment of the age-length key. J. Fish. Res. Bd Can. 34: 317–324

McGurk, M. D. (1986). Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar. Ecol. Prog. Ser. 34: 227–242

Megrey, B. A. (1989). Gulf of Alaska walleye pollock: population assessment and status of the resource as estimated in 1988. In: Wilderbuer, T. K. (ed.) Condition of groundfish resources in the Gulf of Alaska in 1988. NOAA Tech. Memo U.S. Dep. Commerce NMFS F/NWC-165, p. 1–54

Methot, R. D., Jr (1983). Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull. U.S. 81: 741–750

Methot, R. D., Jr (1986). Frame trawl for sampling pelagic juvenile fish. Calif. coop. ocean. Fish. Invest. Rep. 27: 267–278

Methot, R. D., Jr, Kramer, D. (1979). Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull. U.S. 77: 413–423

Miller, T. J., Crowder, L. B., Rice, J. A., Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657–1670

Nishimura, A., Yamada, J. (1984). Age and growth of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as determined by otolith daily growth increments. J. exp. mar. Biol. Ecol. 82: 191–205

Nishimura, A., Yamada, J. (1988). Geographical differences in early growth of walleye pollock, *Theragra chalcogramma*, estimated by back-calculation of otolith daily growth increments. Mar. Biol. 97: 459–465

Nyman, R. M., Conover, D. O. (1988). The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. U.S. 86: 237–250

Parrish, R. H., Nelson, C. S., Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. (N.Y.) 1: 175–203

Peterson, I., Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish Aquat. Sci. 41: 1117–1120

Reed, R. K., Incze, L. S., Schumacher, J. D. (1989). Estimation of the effects of flow on dispersion of larval pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska. Can. J. Fish. Aquat. Sci. Spec. Publ. 108: 280–294

Rice, J. A., Crowder, L. B., Holey, M. E. (1987). Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116: 703–718

Richardson, S. L. (1981). Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull. U.S. 78: 855–876

Shepherd, J. G., Cushing, D. H. (1980). A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. J. Cons. int. Explor. Mer 39: 160–167

Warlen, S. M. (1988). Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull. U.S. 86: 77–90

Wilkinson, L. (1987). Systat: the system for statistics. Systat, Inc., Evanston IL

Yamashita, Y., Bailey, K. M. (1989). A laboratory study of the bioenergetics of larval walleye pollock, *Theragra chalcogramma*. Fish. Bull. U.S. 87: 525–536

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